The Anatomy and Morphology of the Cave-Orthopteran *Macropathus filifer* Walker, 1869*

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Abstract

The purpose of this paper is to record the results of an investigation into the anatomy and morphology of a cave-orthopteran, and correlate it with other members of the Gryllacridoidea both in New Zealand and other parts of the world The anatomy and morphology of *Macropathus filifer* show it to be a typical hemimetabolous insect, although there are minor modifications in the external morphology and in the alimentary and reproductive systems The possession of a median ocellus, the two lateral ones having disappeared, although vestigial nerves are still attached to the protocerebrum, shows that vision is not so essential to the insect

Introduction

Macropathus filifer, a typical member of the Rhaphidophoridae, has been recorded in New Zealand from the northern part of the South Island to the Waikato district in the North Island It is a long, slender insect ranging in length from seven to twelve inches. It is nocturnal in its habits and is usually found in caves, under stones, bark of trees, or in hollow logs. Up to the present the only work carried out on the Rhaphidophoridae in New Zealand has been systematic work in the latter part of the nineteenth century (Walker, 1869; Scudder, 1869; Colenso, 1881; Brunner, 1888; Hutton, 1897; Chopard, 1923; Richards, 1954). Not a great deal of work has been done on the anatomy and morphology of the Orthoptera in other parts of the world so that it is hard to relate the various structures found in *M. filifer.* Perhaps the most extensive worker in this field has been R E. Snodgrass, who has worked more particularly on the Acridiidae. L. Chopard (1920, 1924) and E M. Walker (1919, 1922, 1931) have both made comparative studies of the external genitalia of Orthoptera, and N. Ford (1923) has carried out similar work on their muscles The two principal workers in the Super-Family Gryllacridoidea have been A C. Davis (1927) who worked on the alimentary canal in the Stenopelmatidae, and F G. Maskell (1927), who worked on the anatomy and morphology of a member of the Henicidae; but more extensive study is required of other members of the Orthoptera so that they can be compared and more satisfactory conclusions arrived at.

EXTERNAL MORPHOLOGY

1. The Head Capsule

The head-capsule is of the hypognathous type, the longitudinal axis being vertical, with the mouth-parts directed ventrally Snodgrass (1935a) says the hypognathous condition is more primitive than the forwardly directed prognathous condition, but Walker (1932) claims the early insects were prognathous

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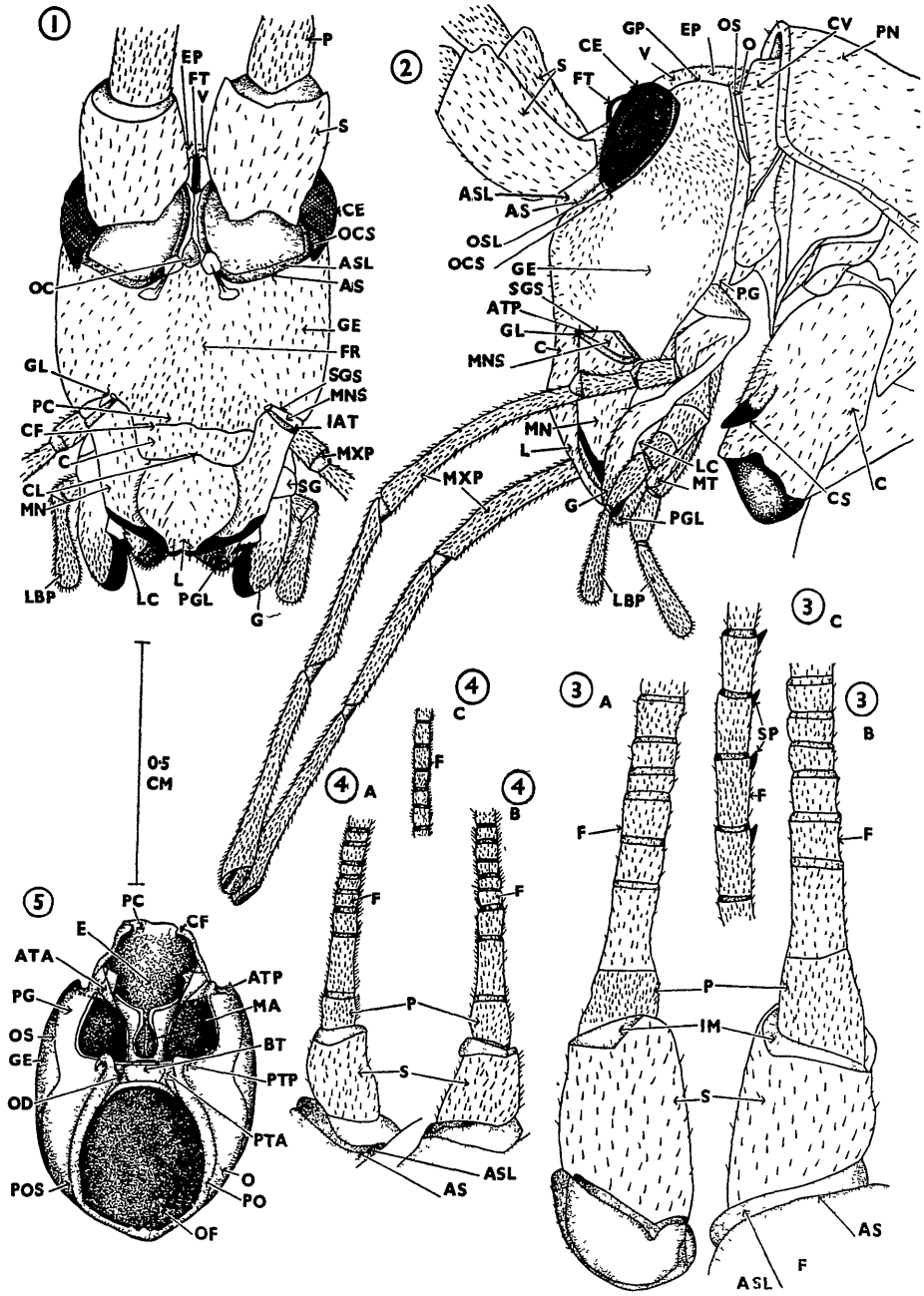


TEXT-FIG. 1. *Head Capsule, Antennae and Tentorium* —FIG 1—Anterior view of head showing sutures. FIG 2—Lateral view of head showing sutures. FIG 3A—Dorsal view of basal segments of right antenna, male FIG 3B—Ventral view of basal segments of right antenna, male. FIG 3C—More distal portion of flagellum of antenna of male showing retrolateral spines FIG 4A—Dorsal view of basal segments of right antenna female. FIG 4B—Ventral view of basal segments of right antenna, female. FIG 4C—More distal portion of flagellum of antenna of female showing lack of spines. FIG 5—Ventral view of head capsule showing tentorium

AS, antennal suture; ASL, antennal sclerite; ATA, anterior tentorial arm, ATP, anterior tentorial pit, BT, body of tentorium, C, clypeus, CE, compound eye CF, clypeal suture, CL, clypeo-labial suture, CS, coxal spine, CV, cervicum, E, median groove of epipharynx, EP, epicranial plate; F, flagellum, FR, frons; FT, fastigium, G, galea; GE, gena, GL, ginglymus, GP, genoepicranial suture, IAT, point of invagination of anterior arm of tentorium, IM intersegmental membrane; L, labrum; LBP, labial palp, LC, lacinia, MA, median aperture, MN, mandible, MNS, mandibular sclerite; MT, mentum, MXP, maxillary palp; O, occiput, OC, ocellus, OCS, ocular suture; OD, occipital condyle; OF, occipital foramen; OS, occipital suture; OSL, ocular sclerite; P, pedicel; PC, postclypeus; PG, postgena, PGL, paraglossa, PN, pronotum, PO, postocciput, POS, postoccipital suture; PTA, posterior tentorial arm; PTP, posterior tentorial pit, S, scape, SG, subgalea; SGS, subgenal suture; SP, spine; V, vertex

and that prognathism in insects to-day is a secondary condition. As *Macropathus filifer* exhibits a number of primitive characters it seems that Snodgrass's statement is probably more correct.

ANTENNAE Figs 3, 4 Situated on the inner side of and partially below the compound eyes; the long, slender, tapering, very flexible sensory flagella are four and a-half times as long as the body in both male and female (excluding ovipositor in females). The antennal sclerite (ASL) forms a ring at the base of each antenna, which is separated from the rest of the head-capsule by the antennal suture (AS) The scape (S) of each antenna articulates with a lateral process on the antennal sclerite and is connected all round to the antennal sclerite by a membrane (IM) In the male (Fig. 3, A, B), the scape is greatly enlarged, about four times the size of the pedicel (P) which, although narrower and shorter than the scape, is broader than the other segments. The third segment, on the dorsal aspect, is narrower, but half as long again as the pedicel, and on the ventral aspect equals the pedicel in length From the fourth segment onwards the segments are unequal in length, although steadily decreasing in size. Some segments are only partly divided; some have a ventral retrolateral spine (SP) in which case the distal part of the segment is swollen and the spine is borne on this swelling; prolateral spines entirely absent This spination of the antennae is found only in the mature male, and there is great variability in the number of spines present (Fig 3, C); it is an example of sexual dimorphism In the female (Fig 4, A, B, C) the antennae are essentially the same except that the scape is not as thick as that of the male and consequently the flagellum is not as long In both sexes the antennae are thickly clothed with setae The long flagellum is easily broken so that the length varies, and in no cases has regeneration of lost segments been observed after an ecdysis.

COMPOUND EYES AND OCELLI Two pear-shaped compound eyes (Fig. 1, CE) lie dorso-laterally to the antennae Between the antero-medial margins of the antennal sclerites on the frons (Fig 1, FR) is a small white pear-shaped structure which is the only ocellus (Fig 1, OC) that survives in *Macropathus filifer* Each eye, in which there are approximately a thousand facets, is surrounded by a chitinous ring, the ocular sclerite (Fig 2, OSL), and where it joins the head-capsule is the ocular suture (Figs 1, 2, OCS) There is a small white area in the dorso-posterior region of each eye where the facets of the eye are much smaller.

CAPSULE Figs 1, 2, 5 The frons (FR) is the median sclerite lying directly anterior to the epicranium (EP), but not separated from it by a suture. Laterally there is no fronto-genal suture to divide it off from the gena; distally it is separated from the clypeus (C) by the invaginations forming the anterior arms of the tentorium, but the greater part of the clypeus is continuous with the frons and the epistomal suture is absent The clypeus is divided ventrally into ante-clypeus (C) and dorsally into post-clypeus (PC) by the clypeal suture (CF). At the junction of the post-clypeus with the mandibular sclerite (MNS) is a concave process that articulates with the ginglymus (GL) of the mandible The post-clypeus is brown and chitinized and the ante-clypeus is white and membranous The cheek is formed by the gena which is separated from the mandibular sclerite by the subgenal suture (SGS); postero-laterally it is separated from the narrow postgena (PG) by the occipital suture (OS); dorso-laterally it is separated from the vertex (V) by another suture unlike anything found

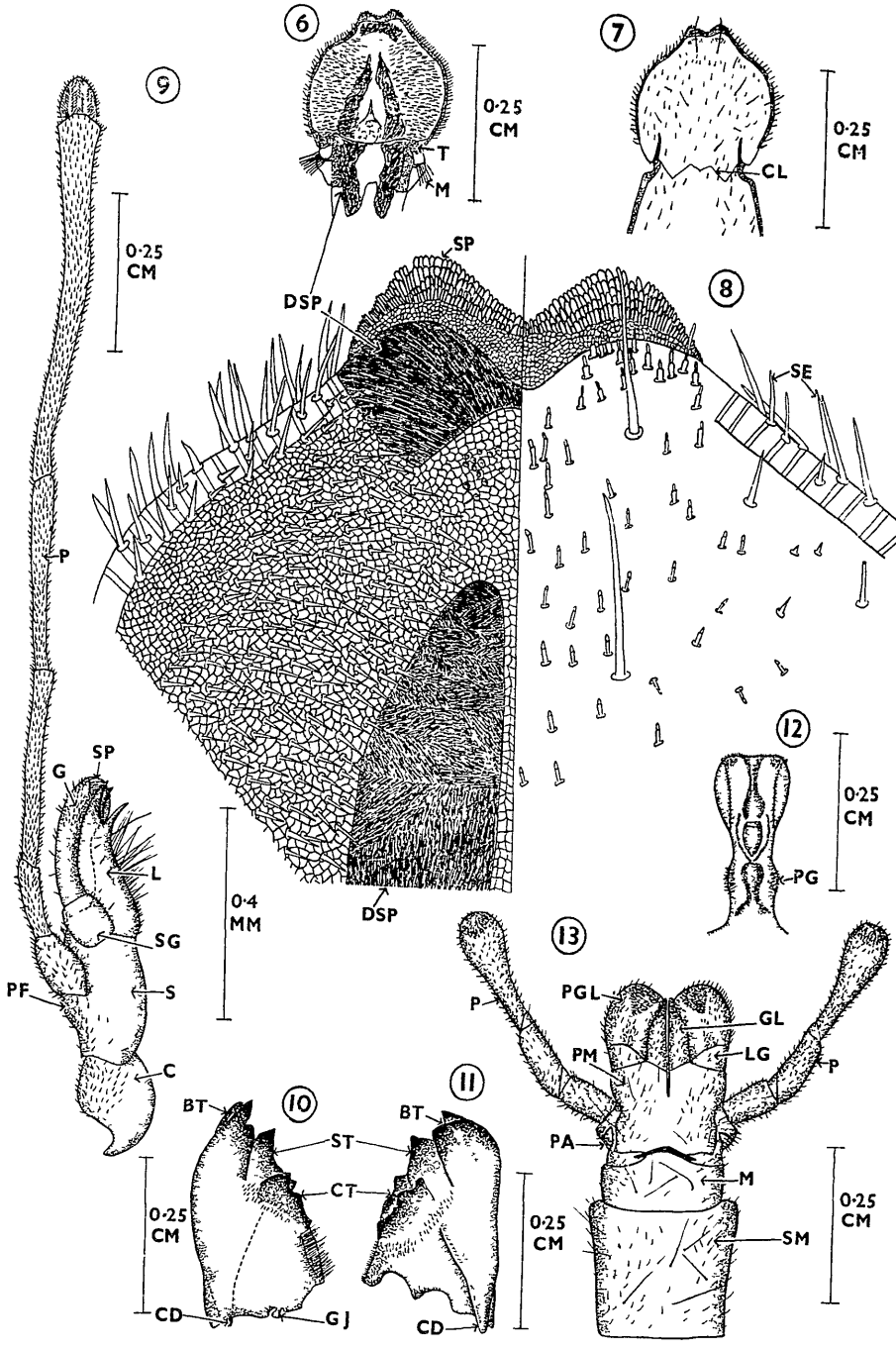
in other Orthopterans so far described, the geno-epicranial suture (GP). The inverted Y-shaped epicranial suture found in most orthopterous insects is not present in *M. filifer*. The fastigium (FT) lies in the median line posterior to the antennae and marks the boundary between frons and vertex. The vertex joins the occiput (O) at the occipital suture (OS) The postocciput (PO) forms the narrow posterior rim of the epicranium to which the neck membrane is attached, and this is separated from the occiput by the postoccipital suture (POS). Ventro-laterally the posterior margin of the postocciput bears a pair of small processes, the occipital condyles (OD) which articulate with the antero-lateral cervical sclerites.

TENTORIUM. Fig. 5. Consists of the body (BT), a pair of divergent anterior arms (ATA) and a pair of divergent posterior arms (PTA). The arms are hollow ingrowths of the head-capsule where roots appear as external pits. The two anterior pits (ATP) separate the gena (GE) from the mandibular sclerite. The two posterior tentorial pits (PTP) are situated ventrally on either side in the postoccipital suture As the head of *M. filifer* is hypognathous the body of the tentorium is short due to the dorso-ventral elongation of the head-capsule The body of the tentorium is broadest posteriorly at the point where the chitinized posterior arms join it and where a posterior bar bounding the occipital foramen (OF) bridges the posterior arms The anterior arms are chitinized along their margins and twisted through a half turn along their length to pass into a broad triangular expansion which joins the head-capsule. At the point of junction of the anterior arms with the body of the tentorium a pair of dorsal arms extend dorsally and anteriorly to the base of each antenna. These arms are thick at their point of origin and then taper along their length to form a triangular-shaped plate at their extremity. Each plate appears to rest on a large apodeme which arises from the posterior margin of the scape of the antenna, but the dorsal arm is not fused to this The attachment of the dorsal arm in *M filifer* is unusual as G. B. Hudson (1945) states that, in all the hypognathous Tettigoniidae she has studied, the dorsal arms are attached to the epicranium in the region of the antennae. A pair of median processes which arise from the base of the anterior arms are directed posteriorly but do not fuse together; posterior to them and still in the anterior part of the body of the tentorium is a median aperture (MA) through which the circumoesophageal connectives pass. The principal function of the tentorium is for the attachment of gnathal muscles, but it also affords support to the fore-intestine and the brain.

2 MOUTH PARTS

These have labrum, mandibles, maxillae, labium and hypopharynx all well developed Though of an omnivorous feeder, they are more particularly adapted for biting and tearing.

LABRUM. Figs. 6, 7, 8. Borne on the ante-clypeus to which its outer surface is attached by the clypeo-labral suture (Fig 7, CL), it consists of a broad flat lobe with the distal margin notched in the mid line and bearing several rows of sensory papillae (Fig 8, SP), laterally the margin is strongly chitinized and provided with a fringe of setae (Fig. 8, SE); the outer surface has a number of basiconic sensillae scattered over it The inner surface is thickly clothed with setae and has a median groove towards which nearly all the setae are directed; on either side of this groove, and anterior to it, is a dense mass of



TEXT-FIG. 2 *Mouth Parts.*—FIG. 6—View of labrum inner surface FIG. 7—View of labrum, outer surface FIG. 8—Labrum enlarged. Left half shows inner surface and right half outer surface FIG. 9—Maxilla. FIG. 10—View of mandible, outer surface FIG. 11—View of mandible, inner surface FIG. 12—Hypopharynx FIG. 13—Labium

BT, bifid tooth; C, cardo, CD condyle, CL, clypeo-labial suture, CT, 6-cusp tooth, DSP, dendritic sensory papillae, G, galea, GJ, ginglymus joint GL, glossa, L lacinia, LG ligula, M, mentum, P, palp, PA, palpiger, PF, palpifer, PG, bristles and basiconic sensillae, PGL, paraglossa, PM, prementum; S, stipes; SE, setae, SG, subgalea, SM, submentum, SP, sensory papillae, ST, single sub-apical tooth, T, torma

dendritic sensory papillae (Fig 8, DSP); dendritic papillae are also situated near the distal margin and are probably concerned with taste. The inner surface is continuous with the inner membranous surface of the clypeus and forms the epipharynx. The inner surface of the ante-clypeus is less thickly clothed with hairs than the labrum, and is separated from it by two small chitinous bars, the tormae (Fig. 6, T).

MANDIBLES. Figs. 10, 11. Very strongly chitinized; situated one on either side of and behind the labrum; strongly toothed with an apical bifid tooth (BT) extending one-third down, a single subapical tooth (ST) extending from one-third to one-half down, and a sub-basal tooth (CT) with six cusps between one-fifth and two-thirds up The proximal surface carries a thick clothing of setae and a blunt projection from the posterior surface. Mandibular sclerite small, continuous with the post-clypeus, separated from the gena by the invagination forming the anterior arm of the tentorium of its side, and the subgenal suture The mandible articulates with the head-capsule by an anterior ginglymus (GJ) and a posterior condyle (CD) The ginglymus articulates with a concave process situated at the point where the post-clypeus and mandibular sclerite are joined. The condyle articulates with an acetabulum on the ventral margin of the occiput.

MAXILLAE. Fig. 9. Behind the mandibles are paired maxillae which, excluding their palps (P), are slightly larger than the labium. The cardo (C) is triangular in shape, with the length to the width as 1 1:1, and articulates with the rim bordering the lateral margin of the occipital foramen. Distal to each cardo is the stipes (S), twice as long as broad and a third as long again as the cardo. Externally each stipes carries a five-segmented maxillary palp (P), which is thickly clothed with setae and very sensitive to touch and chemical senses. Each palp arises from a palpifer (PF), formed from the outer distal portion of the stipes by constriction from the rest as a separate lobe. First two palpal segments short, last three long, of which the terminal segment is club-shaped. The relationship of the length of each segment to the palp is 7·7 20:20·44. Proximally the stipes carries a lacinia (L) and galea (G) which are both weakly chitinised. At the tip of the lacinia is a bifid spine, and beneath this spine an articulated spine. The internal surface of the lacinia has numerous long setae. The galea consists of two joints, a proximal one, the sub-galea (SG) which is short and slightly swollen, and a distal one which is elongated and at its tip bears an area of sensory papillae (SP) behind which is a group of setae

LABIUM Fig. 13 The submentum (SM), mentum (M), prementum (PM), palp (P), ligula (LG), glossa (GL) and paraglossa (PGL) are all present. The submentum is large, length related to width as 1 1 2, it articulates with the rim at the anterior margin of the occipital foramen and also with the small mentum Mentum wider than long, as 2 3.1 The prementum, which is wider than long as 1 4:1, lies in front of the mentum and is cleft anteriorly for a third of its length. Submentum·mentum prementum are related in length as 2 2 1·1 5 On each side of the prementum is a palpiger (PA) which bears a three-segmented labial palp, the ratio of the length of each segment to the total length of the palp being 21.30·50. Both palps are clothed with setae; last segment of the palp is club-shaped and more heavily clothed with setae towards its apex, where the setae form a series of whorls all directed inwards towards the apex Antero-lateral to the prementum are two small ligulae, each of which bears a large thick

paraglossa; at the tip of the paraglossa is an area of sensory papillae. Paired glossae are borne on the anterior border of the prementum, and are clothed with setae. They taper towards their tips, and, as in the paraglossae, have an area of sensory papillae at their anterior ends.

HYPOPHARYNX. Fig. 12. This is an unpaired tongue-like organ which forms the lower border of the pharynx proper. It is greatly swollen, soft and spongy and is strengthened by a chitinous framework. Its posterior wall is reflected into the ventral wall of the labium at the base of the prementum, from where it is produced forwards into a lobe which lies above the glossae and paraglossae, beneath this lobe is the opening of the salivary duct. Near the base of the hypopharynx on each side is a lobe bearing bristles and basiconic sensillae (PG) According to Snodgrass (1928) these setae are supposed to be pervious to chemical stimulae and are regarded as receptors of taste or odour

3 THORAX AND THORACIC APPENDAGES

TERGUM. The tergum has the three plates, pronotum, mesonotum and metanotum, clearly defined.

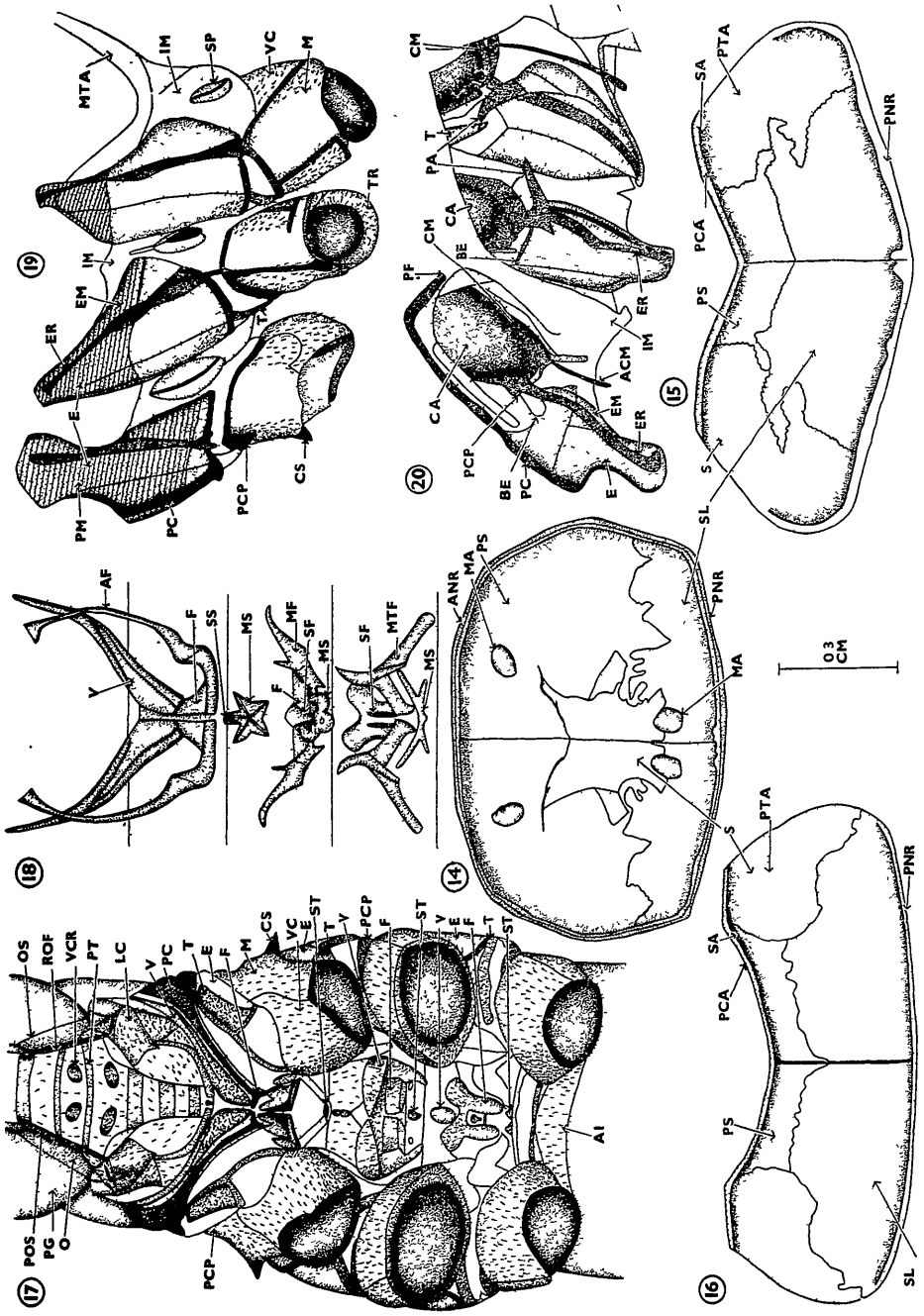
Pronotum. Fig. 14 Broad, overlapping most of the pleura, but not as broad as either the mesonotum or the metanotum. The anterior margin is rounded, allowing the neck and posterior portion of the head to be withdrawn beneath it. The pronotum is divided into three definite regions—anteriorly the prescutum (PS), medianly the scutum (S) and posteriorly the scutellum (SL) There is no precostal acrotergite present on the pronotum, but both anterior (ANR) and posterior (PNR) notal ridges are present The structure termed postnotum by Snodgrass, 1929, and postscutellum by Martin, 1916, is not present

Mesonotum Fig. 15 Broader than the pronotum and overlapping part of the pleura. The anterior margin bears the precostal acrotergite (PCA) and is overlapped by the pronotum Anteriorly it is divided into an anterior prescutum, a lateral scutum and a posterior scutellum There is no postnotum

Metanotum Fig 16. Equal in width to the mesonotum by which it is overlapped anteriorly. Its anterior border bears the precostal acrotergite (PCA). It is divided into an anterior prescutum, a lateral scutum and a posterior scutellum There is no postnotum

In the mesonotum and metanotum the precostal acrotergite separates the anterior part from the remainder of the plate. This anterior part forms the submarginal antecosta (SA) while the poserior part forms the postcostal area (PTA).

PLEURON. Figs 19, 20 The pleuron consists of the sclerites lying between the tergum and sternum forming the lateral wall of the thoracic segment. It is composed of two sclerites, the episternum (E) or anterior sclerite, and the epimeron (EM) or posterior sclerite Du Porte (1919) states that in Orthoptera the propleural regions are not crowded out but are overgrown by the pronotum. In *Macropathus filifer* a small portion only of the pleuron can be seen below the lateral margin of the pronotum, but in the mesothorax and metathorax the greater part of the pleuron becomes visible The three segments of the tergum are joined to the three pleural segments by three membranes (PM) which indicate where the pro-, meso-, and metanota end. Each membrane overlaps its pleural segment and forms a sac through which a needle can be passed.



TEXT-FIG 3. *Thorax*.—FIG 14—Pronotum; inner surface showing sutures FIG 15—Mesonotum, inner surface showing sutures FIG 16—Metanotum inner surface showing sutures FIG. 17—Sternal region: external FIG 18—Sternal region internal FIG. 19—Pleural region external FIG 20—Pleural region internal

A 1, abdominal stermite; ACM, apodeme attached to coximarginal sclerite, AF, arm of furca, ANR, anterior notal ridge, BE, base of episternum, CA, coxal aperture, CM, coximarginal sclerite, CS, coxal spine, E, episternum EM, epimeron, ER, entopleural ridge, F, furcasternite, IM, supporting membrane (inter-segmental), LC, lateral cervical sclerite, M, meron, MA, point for muscle attachment, MF, medifurca; MS, median spina, MTA, membrane connecting thorax to first abdominal segment, MTF, metafurca, O, occiput, OS occipital suture, PA, pleural arm, PC, precoxale, PCA, precostal acrotergite, PCP, pleural coxal process, PF, point where precoxale fuses with furcasternite; PG, postgena, PM, membrane overlying pleura, PNR, posterior notal ridge, POS, postoccipital suture, PS, prescutum, PT, prosternite; PTA, postcostal area, ROF, rim at margin of occipital foramen, S, scutum, SA, submarginal antecosta, SF, stalk for attachment to furcasternum; SL, scutellum, SP, spiracle; SS, stalk for attachment of spinasternum, ST, spinasternite; T, trochantin; TR, trochanter, V, verasternite; VC, veracoxa, VRC, ventral cervical sclerites.

The pleuron in most insects bears three inwardly directed processes for the attachment of muscles. These usually comprise a dorsal pleural wing process for articulation of the wing, a lower lateral pleural coxal process (PCP) with which the coxa articulates; the pleural suture and pleural ridge (entopleuron) (ER) extending through it; and the pleural arm (PA) which is situated a short distance above the coxal process, projecting inward and downward from the entopleuron to rest against the furca and thus form an internal connection between the pleuron and sternum.

Macropathus filifer being apterous lacks the pleural wing process, and in the propleura the pleural arm is missing from the entopleuron. In the three segments the epimeron is considerably reduced, while the episternum is large. The episternum is subdivided longitudinally and has a thickened ventral margin. In the prothorax only it is fused with the precoxale which passes ventrally to unite, but not fuse, with the sternum and thus form a bridge connecting the episternum to the sternum. The precoxale is absent from the mesothorax and metathorax.

Articulating with both the antero-mesal margin of the coxa and the anterior end of the thickened ventral margin of the episternum is a small, transversely placed, triangular-shaped sclerite, the trochantin (T)

Between the thoracic segments, situated within the intersegmental membrane, are the intersegmentalia, the sclerites which surround the spiracle The third thoracic spiracle belongs to the first abdominal segment Snodgrass (1935a) says that the first and second spiracles belong to the mesothorax and metathorax respectively, although they often "migrate forward during development and come thus to have a definitive position in the secondary intersegmental membranes or in the posterior parts of the segments preceding them. The mesothoracic spiracles particularly are subject to this anterior migration and hence often occur in larval or adult insects on the sides of the prothorax, for which reason they are frequently called the 'pro-thoracic' spiracles " In *Macropathus filifer* the spiracles have moved forward into the posterior part of the prothoracic and mesothoracic intersegmental membranes and the mesothoracic spiracle is much larger than the metathoracic one.

STERNUM. Figs 17, 18 The prosternum of *Macropathus filifer* is divided into four parts—prosternite (PT), verasternite (V), furcasternite (F) and spinasternite (ST) The prosternite is absent in the mesosternum and metasternum but the other three sclerites are present Martin (1916) says the sternum of insects is "composed of five subdivisions," but the fourth division, the postfurcasternite, is not present in *M. filifer*.

Prosternum. Anteriorly this consists of a poorly chitinized area formed from a membrane with rings of chitin embedded in it (PT), which extends into the cervicum. Situated immediately posterior to this is the verasternite (V), which is produced at each anterior corner into a long arm directed antero-laterally. The verasternite is connected by a narrow membrane with the precoxale (PC), which is fused to the episternum (E) forming the precoxal bridge There is no postcoxale. The furcasternite is situated directly behind the verasternite, from which it is separated by a membrane. Anteriorly it is divided into two short processes and internally it bears the furca (AF) which consist of two long, slender, anteriorly directed arms, each terminating in a thin plate. The spina-

sternite is very small and oval and bears the single, median, star-shaped spine (MS), consisting of five approximately equal arms.

Mesosternum. The verasternite, furcasternite and spinasternite are all fused together forming one large plate. The posterior margin bears the medifurca (MF) and the median spina. There is no precoxale. The medifurca consists of a stalk attached to the furcasternite and bearing two laterally diverging arms, each one of which bears three processes directed anteriorly, antero-laterally and posteriorly respectively The antero-lateral of these processes is the largest, and it articulates with the pleural arm (PA) of the entopleuron on its side. The spina is attached by a stalk to the spinasternite and bears five arms—two large ones antero-laterally, two small ones anteriorly, and one large one posteriorly.

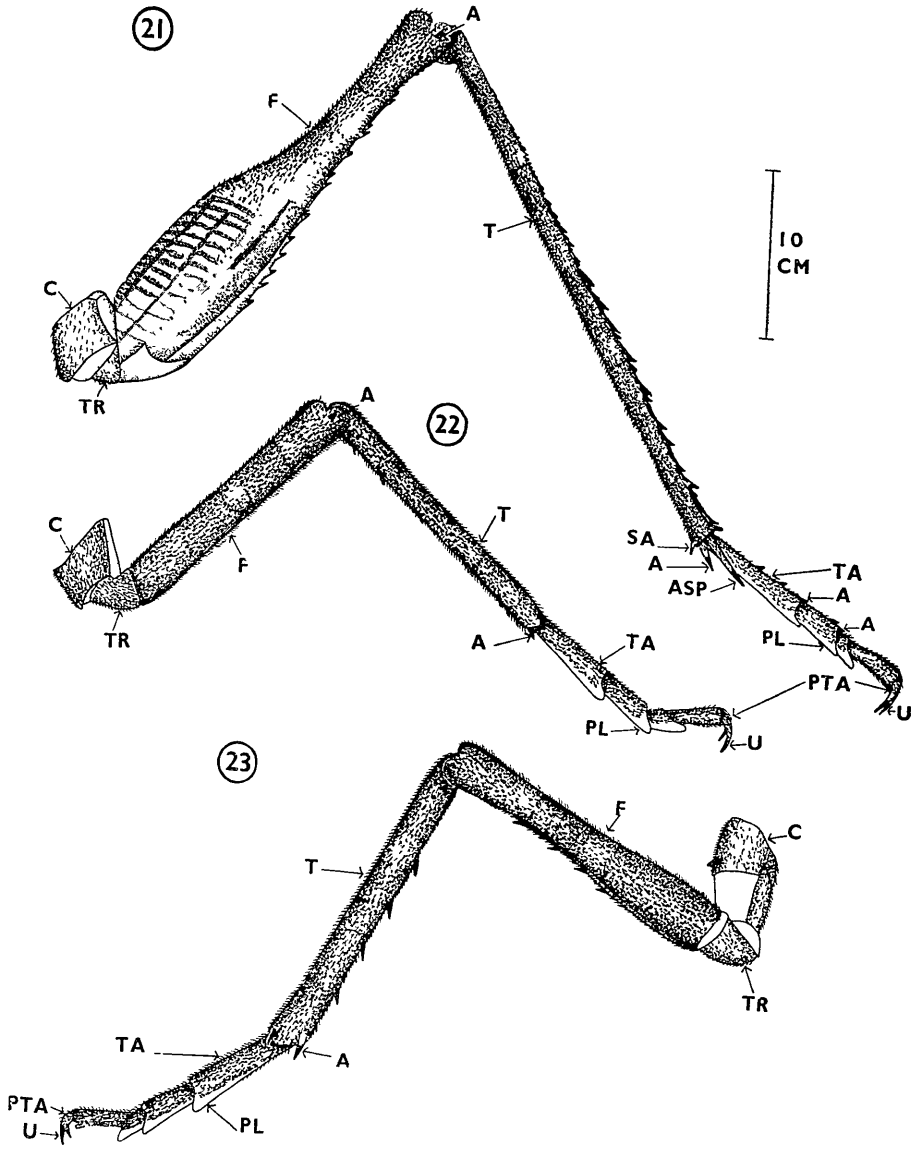
Metasternum. The small oval verasternite lies partly in a median depression of the furcasternite from which it is separated by a membrane. The furcasternite is large and bears two anteriorly directed arms. The spinasternite is reduced to two very small sclerites at the base of the furcasternite. The metafurca (MTF) which is attached to the furcasternite consists of a stalk bearing two laterally diverging arms. Each arm bears three processes directed anteriorly, postero-laterally and posteriorly respectively. The postero-lateral process is the longest, and it articulates with the pleural arm of the entopleuron Attached to the spinasternite is the median spina consisting of five arms—two long ones directed antero-laterally, two shorter ones postero-laterally, and a much shorter one posteriorly. Of the spinasternite Martin (1916) says, "It is so variable in position that it is very hard to tell to which segment the spinasternite belongs, but it probably belongs to the segment in front of it, as no spinasternite has ever been described as occurring in front of the prothoracic verasternite." In *M. filifer* this is true, for the spinasternite is definitely the last sclerite of each segment In contradiction to Snodgrass (1935a), who states " It should be observed that the metasternum never has a spinasternite, because the third intersternite either is suppressed or becomes the acrosternite of the first abdominal sternum", *M. filifer* has a small spinasternite to which is attached a well developed spina.

Cervical Sclerites. Fig. 17 There are three pairs of lateral cervical sclerites (LC). The anterior one is oblong and in front articulates with the margin of the occipital foramen to which its anterior end is connected by a membrane Posteriorly it articulates with the forward edge of the triangular-shaped second sclerite, and this in turn articulates with the third sclerite which is the largest of the three. This third sclerite bears a large postero-lateral arm and articulates behind with the precoxal bridge

There are two pairs of oval shaped ventral sclerites (VC) embedded in the membrane of the neck, the posterior pair being more strongly chitinized than the anterior pair

Legs Figs. 21–23. The legs are long and slender The fore and middle limbs are about the same length, but the hind limb is much longer and more powerfully constructed for jumping. Each leg consists of six articulating segments—coxa (C), trochanter (TR), femur (F), tibia (T), tarsus (TA) and pretarsus (PTA) Crampton (1923) states, "The trochanter articulates with the coxa but does not articulate with the femur in any insect I have examined, and it is quite possible that the trochanter may be a constricted off portion of the femur." Maskell (1927) says, "In the metathoracic legs of *Hemideina* the

trochanter is firmly attached to the femur, there being no articulation between them. But in the prothoracic and mesothoracic legs there is a small but distinct articulation between trochanter and femur". In *Macropathus filifer* there is a definite articulation between the trochanter and femur in all three pairs of legs. It is especially noticeable in the metathoracic legs where the articulation is easily broken and the legs lost, while the coxa and trochanter remain attached to the thorax Auditory organs are lacking on the prothoracic tibia, and because of this there is no area of small spines on the femur of the hind leg, nor a file



TEXT-FIG. 4 *Thoracic Appendages.*—FIG. 21—Left hind leg FIG 22—Left middle leg FIG 23—Left fore leg

A, apical spine, ASP, apical spur, C, coxa, F, femur, PL, pseudopad, but euplantula lacking, PTA, pretarsus, SA, subapical spine, T, tibia, TA, tarsus, TR, trochanter, U, unguis

on the second abdominal segment to be rubbed together to make the stridulating organ characteristic of the Henicidae and many of the Rhaphidophoridae Another characteristic of *M. filifer* is the lack of real euplantulae, or pads, on the tarsi.

Coxa Proximally the coxa articulates with the pleural coxal process (Figs. 19, 20, PCP) and the trochantin (T) along its heavily chitinized anterior margin, and distally it articulates with the trochanter. The coxae of both the meso- and metathorax are partly subdivided into proximal and distal regions, veracoxa (Fig. 17, VC) and meron (M) respectively. The suture which marks this subdivision is a continuation of the pleural suture. Martin (1916) says, "The meron when present appears to be developed in the meso- and sometimes in the metathorax I have never observed its presence in the prothorax The coxa was probably originally one undivided sclerite and the meron has been derived from it secondarily" The fore coxa only is armed with a sharp spine on the forward edge. All the coxae are clothed with setae.

Trochanter The trochanter of each leg is a small triangular-shaped sclerite clothed with setae.

Femur The fore and middle femora are grooved below, with the edges of the grooves rounded The middle femur bears a short, stout, apical prolateral spine and a smaller similar apical, retrolateral spine Hutton (1896) states that there is "a short, stout, apical spine on the inner side" and makes no mention of the retrolateral spine which I have found in all specimens examined. The hind femur is deeply grooved below with edges strongly carinate The spines along the margin of the ventral grooves are unequally spaced and vary in size, the proximal ones being very small and the distal ones the largest All the femora are heavily clothed with short golden setae.

Tibia The hind tibia (Fig 21) bears a pair of apical spurs (ASP), a pair of apical spines (A) and a pair of subapical spines (SA) The hind tibia, in contrast to the hind femur, is rounded ventrally and grooved dorsally, though it is not as deeply grooved as the femur. The spines along the margin of the groove are large at the distal end and taper to a very minute size at the proximal end In some specimens the large spines along the length of the hind tibia are subtended by very small spines at their bases All the tibiae, and on the hind tibiae the apical spurs as well, are clothed with setae

Tarsus. Each tarsus proper consists of four segments, and there is also a pretarsus The most proximal segment is not quite so long as the second and third together. The third segment is very short The fourth segment is longer than the second and third, but not so long as the first The tarsi on the dorsal surface are rounded proximally, but depressed distally rather like a spoon They lack euplantulae and are covered with a thick clothing of setae In the hind tarsus the first and second segments each have a pair of apical ventral spines The pretarsus distally bears a pair of claws (ungues) (Figs 21, 22, 23, U)

4. The Abdomen

The abdomen of a typical orthopterous insect consists of eleven segments, but this number is often reduced due to modifications and complications in the external genitalia. In the male of *Macropathus filifer* there are ten tergites, the supra-anal plate being fused to the tenth tergite so that there is no definite eleventh tergite present Ventrally there are nine sternites, and the hypandrium

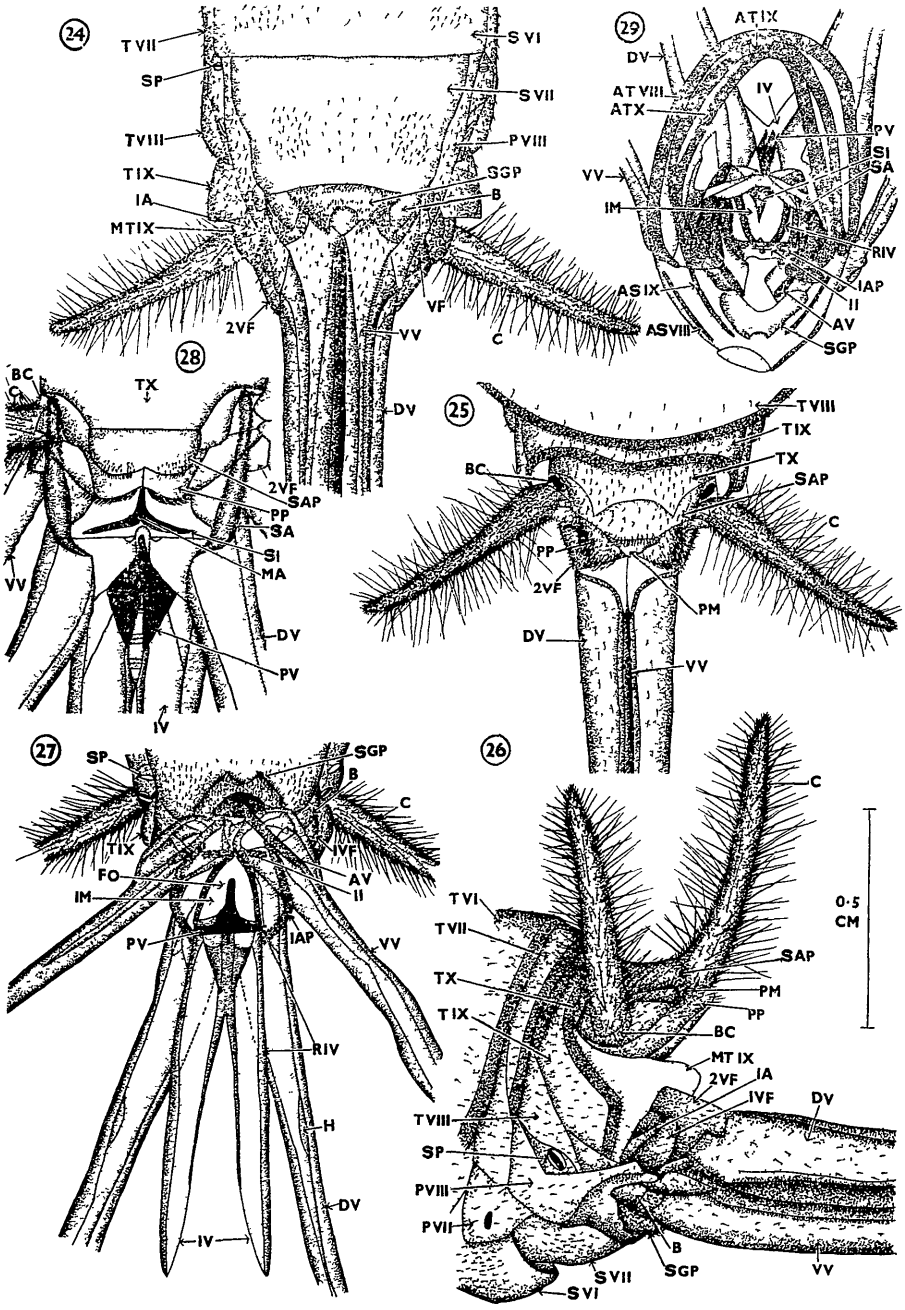
(sub-genital plate) is borne on the ninth sternum. In the female there are ten tergites. The supra-anal plate is fused to tergite ten as in the male There are seven sternites and the sub-genital plate is attached to sternite seven.

The terga and sterna are undivided shields linked together by intersegmental membranes, while the pleura are membranous and lacking in clearly differentiated sclerites. The first abdominal tergum is joined to the metathorax (metanotum) by an intersegmental membrane, but the first abdominal sternum is firmly attached to the metasternum. The pleura and sterna are thickly clothed with setae, but there are far fewer setae on the terga. The eight abdominal spiracles are located in the tergo-pleural membranes below the abdominal terga.

5. External Genitalia

FEMALE. These consist of the vulva, or genital aperture, the subgenital plate, and three pairs of processes, the gonopophyses or valvulae, which together form the ovipositor. The genital aperture is situated on the seventh abdominal sternum (Fig. 24, S VII) and is covered by the subgenital plate (SGP) which is a backward prolongation of the sternum. The dorsal valvulae (Figs. 25, 26, DV) are the longest and overlap the ventral ones (Figs. 24, 26, VV), the tips of which curve up to meet them. The inner valvulae (Fig. 27, IV) lie alongside the inner faces of the ventral ones, but are much shorter than either of the other two pairs. There is very little difference in the length of the dorsal and ventral valvulae and they are approximately the same length as the body from vertex to anus. The dorsal and ventral valvulae completely enclose the inner valvulae.

The Rhaphidophoridae are regarded as possessing some of the most primitive types of ovipositors In *Macropathus filifer* the ovipositor is approximately ovoidal at the base and the blades become increasingly compressed distally. Each dorsal valvula possesses a hook (Fig 27, H) on the ventral surface for sliding over the serrated chitinized outer edge of the corresponding ventral valvula so that the valvulae do not part company, but are held together and their only movements are backwards and forwards The dorsal valvulae meet along their mid-dorsal line, the ventral valvulae along their mid-ventral line. The ovipositor is roughly sabre-shaped with a marked dorsal curve In the young animal the developing ovipositor is a creamy colour and very soft, but as it develops the colour intensifies to a deep red brown at the tip and round the edges of the valvulae. When the colour is fully developed the animal is sexually mature With the deepening of colour, chitin is deposited most strongly round the edges of the dorsal and ventral valvulae The inner valvulae are white with a thin band of chitin, the rami (Fig 27, RIV), round their edges These are connected by a strengthening bar, the pons valvularum (Figs. 27, 28, 29, PV), which extends across the intervalvular membrane (Figs 27, 29, IM), a fold of integument connecting the inner valvulae for a short distance from the base Between the bases of the dorsal valvulae and fused with them is a median sclerite, the superior intervalvula (Figs. 28, 29, SI), which bears a median vertical apodeme (Fig. 28, MA) for attachment of the principal muscles concerned with the movements of the ovipositor. Another median sclerite, the inferior intervalvula (Figs. 27, 29, II), is situated on the ventral surface at the base of the intervalvula membrane The rami of the inner valvulae are connected with the inferior intervalvular and also with the inferior apophysis (Figs. 27, 29, IAP), a ventral process arising from the base of each dorsal valvula A similar larger process,



TEXT-FIG 5. *External Genitalia. Female* FIG 24—Ventral view terminal abdominal segments FIG 25—Dorsal view terminal abdominal segments FIG 26—Lateral view terminal abdominal segments FIG 27—Ventral view, valves of ovipositor opened out showing supporting apodemes FIG 28—Dorsal view, valves of ovipositor opened out showing supporting apodemes FIG 29—Posterior interior view terminal abdominal segments, showing skeletal structure of genitalia

AP VIII IX, X apodemes of pleurites VIII IX, X, AS VIII, IX, poorly chitinized apodemes of sternites VIII, IX; AT VIII, IX, X, apodemes of tergites VIII, IX, X, AV, apodeme of ventral valve, B, basivalvula, BC, basal segment of cercus, C, cercus, DV, dorsal valve, FO, fenêtres ovales II, hook for articulation with ventral valve, IA, intersegmental apodeme, IAP, inferior apophysis, II, intervalvula, IM, intervalvular membrane, IV, inner valve, MA, median apodeme, MT IX membrane tergite IX, P VII, VIII, pleurite VII, VIII, PM, perianal membrane, PP, paraproct, PV, pons valvularium, RIV, ramus of inner valve, S VI, VII, sternite VI, VII, SA, superior apophysis, SAP, supra-anal plate, SGP, subgenital plate, SI, superior intervalvula, SP, spiracle, T VI, VII, VIII IX, X, tergite VI, VII, VIII, IX, X, 1VF, first valvifer, 2VF, second valvifer, VV, ventral valve

the superior apophysis (Figs 28, 29, SA), projects forward into the haemocoele from the dorsal basal region of each valvula Both these pairs of apophyses serve for muscle attachment.

The inner valvulae roof over the passage along which the eggs are passed

The ventral valvulae arise from the posterior margin of the eighth sternum Each consists of a short basal segment, the basivalvula (Figs. 24, 26, 27, B), and a longer shaft The basivalvulae are distinct, though not heavily chitinized, and are not wholly concealed by the rather small subgenital plate Between the basivalvula, the ninth tergite (Fig 24, T IX) and the base of the dorsal valvula is the subtriangular first valvifer (Figs 24, 26 1VF). Dorsal to this is the second valvifer (Figs 24, 26, 2VF). These valvifers form the antero-lateral part of the ninth sternum

The broad proximal portion of the dorsal valvulae passes imperceptibly into a longer, more slender, distal portion not separated by a suture so that no basivalvulae are recognisable.

The eighth sternum is prolonged caudad as the subgenital plate covering the vulva and bases of the ventral valvulae On the ventral surface of the subgenital plate is a flap of tissue closing the aperture of the genital chamber. The subgenital plate (Fig 24 SGP), which is obtuse-angled laterally, and deeply emarginate distally, appears constant in shape in all the animals I have examined. It is thickly clothed with setae

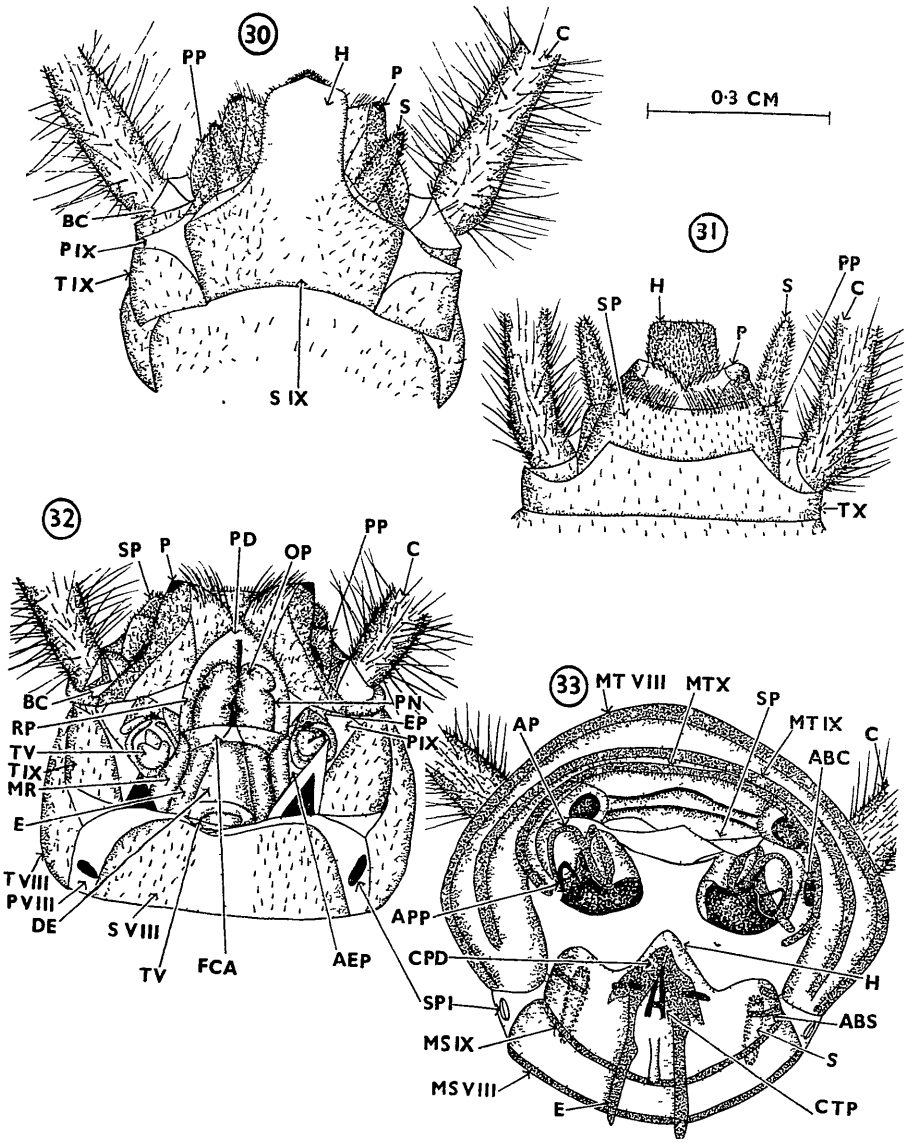
The supra-anal plate (Fig 25, SAP), though well developed, is not divided transversely into two sclerites—i e., there is no separate eleventh tergite and the plate is not sharply marked off from the tenth tergite (Fig. 25, TX). The shape of the supra-anal plate is not constant but varies between two extremes, one of which is rounded and notched in the centre (Fig. 28, SAP), while the other is obtuse-angled laterally and truncated terminally (Fig 25, SAP) Many intermediate stages occur, some straight, some slightly concave, and others slightly convex.

The paraprocts (Fig 25, PP) are well developed, but little chitinized, and are clothed with brown setae

The long, flexible cerci (Figs 24, 25, C) taper from a stout base to a slender apex. There is a basal segment (Fig 25, BC) at the base of each cercus The cerci are clothed with long and short setae and are similar in both sexes

MALE The supra-anal plate (Fig. 31, SP) is well developed and fused with the tenth abdominal tergite (TX). As in the female its shape is not constant. It may be either concave or convex terminally or of an intermediate stage between these two extremes The ninth sternum (Fig 30, S IX) is undivided, and on each side disto-laterally bears a terminal stylus (Figs. 30, 31, S). The cerci (Figs 30, 31, C), which are as already described for the female, are not modified to function as claspers

Situated in the large membranous area between the paraprocts (Figs. 31, 32, PP) and the ninth sternum is the penis (Fig. 32, PN). This organ itself is almost entirely membranous and is divided into four lobes, two dorsal and two ventral On the tips of the two upper ones are the openings of the male genital ducts (Fig 32, OP), clearly demarcated by their chitinized margins. Arched over the base of the penis is the hood-like pseudosternite (Fig. 32. PD) the cavity of which forms a sheath into which the penis may be retracted. It serves for the insertion of muscles concerned with the movements of the penis



TEXT-FIG 6 *External Genitalia, Male* FIG 30—Ventral view genitalia FIG 31—Dorsal view genitalia. FIG 32—Ventral view genitalia—hypandrium removed to expose structure beneath FIG 33—Posterior interior view of terminal abdominal segments showing skeletal structure of genitalia

ABC, apodeme of basal segment of cercus; ABS, apodeme of basal segment of stylus, AEP apophysis of endoparamere, AP, apodeme of paramere, APP, apodeme of paraproct, BC, basal segment of cercus, C, cercus, CPD, chitinous structure of pseudo-sternite, CTP chitinized tubes of penis; DE, ductus ejaculatorius, E, endopophysis, EP, endoparamere, FCA, feebly chitinized arch connecting rami; H, hypandrium (subgenital plate); MR, muscle attached to ramus, MS VIII, IX, membrane sternite VIII, IX; MT VIII, IX, membrane tergite VIII, IX, OP, opening of penis, P, paramere (ectoparamere), P VIII, IX, pleurite VIII, IX, PD, pseudosternite, PN, penis, PP, paranal plate (paraproct); RP, rami of pseudosternite, S, stylus, S VIII, IX sternite VIII, IX, SP, supra-anal plate; SPI, spiracle, T IX, X, tergite IX, X, TV, tube of vesiculae seminales

This arch is prolonged on each side into a pair of arms, the rami (Fig. 32, RP), which are connected with one another ventrally by a feebly chitinized arch (Fig 32, FCA). The rami are produced inwardly into two processes, the endapophyses (Fig. 32, E), which are large and well developed and serve for the attachment of further muscles controlling the movements of the penis

The parameres (Figs 31, 32 P), which are dorso-terminal in position, are chitinized more heavily on their outer sides and their inner surfaces are thickly clothed with long brown setae At the tip of each paramere is a dark brown spot of chitin. The upper external portion of the paramere is the ectoparamere. The bases of the parameres unite to form a plate, the endoparemere (Fig 32, EP), attached to which, on either side of the pseudosternite, is an apophysis (Fig. 32, AP)

On either side of the parameres and beneath the supra-anal plate lie the paraprocts, which are lobe-like structures, but little chitinized and clothed with brown setae.

The hypandrium (Fig. 30, H) (subgenital plate) is part of sternite nine and bears two short, stout styli clothed with short brown setae. The hypandrium covers over all the genitalia except the parameres. The tip of the ventral surface of the hypandrium is brush-like, thickly clothed with brown setae, and projects beyond the dorsal surface of the plate.

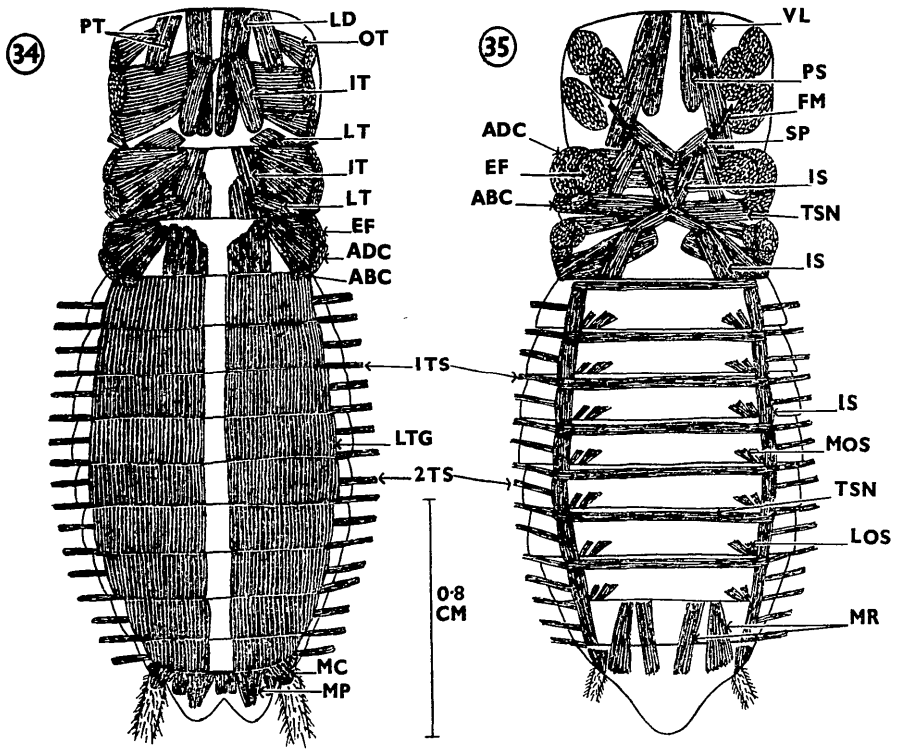
MUSCULAR SYSTEM

HEAD Fig. 39 The musculature of the head of *Macropathus filifer* is made up primarily of muscles from the mouth parts and antennae, most of which have their point of origin on the tentorium Each antenna is moved by two pairs of muscles, the levators (LA) and depressors (DA) of the antenna, which are inserted on the base of the scape Both pairs of muscles arise on the tentorium, but the levators are inserted on the dorsal side of the base of the scape, while the depressors are inserted on its ventral margin Arising dorsally from the base of the scape are two muscles, the flexor (FF) and extensor (EF) of the flagellum, which are attached to the base of the pedicel Running from the pedicel to the most distal portion of the flagellum along the outer margin of the tracheal trunks are two narrow bands of extrinsic smooth muscle fibres These bands give extra flexibility to the flagellum, enabling it to bend in any direction This extra flexibility due to the extrinsic muscles has probably been secondarily acquired because of the cave-weta's mode of life in caves where sensitivity to environmental conditions is of primary importance

The mandibles are supplied with two muscles each inserted on an apodeme. The abductor (ABM) is a small muscle arising on the ventral part of the post-gena and the postero-ventral half of the gena, and inserted on the abductor apodeme close to the outer margin of the mandibular base, near the posterior articulation The adductors (AM) are two sets of fibres, one arising on the dorsal wall of the cranium, between the compound eyes and occiput, and the other on the lateral wall of the cranium Both sets of fibres are inserted on the median apodemal plate

The maxillae are well supplied with muscles, having muscles that move the appendage as a whole, and muscles that move the terminal lobes and palp. The promotor of the cardo arises on the post-gena, and is inserted on the base of the cardo. The adductors (AC) of the cardo arise on the posterior end of the

anterior arm of the tentorium, one inserted on the inner face of the cardo, the other on the outer face. The adductor muscles of the stipes (AS) arise on the posterior end of the anterior arm of the tentorium and are inserted on the inner side of the stipes. The muscles of the galea, lacinia and the intrinsic muscles of the palp, enable them to move independently of the whole maxilla.



TEXT-FIG. 7. Muscular System.—FIG. 34—Inner surface of terga showing dorsal muscles—alary muscles removed. FIG. 35—Inner surface of sterna showing ventral muscles

ABC, abductor of coxa, ADC, adductor of coxa, EF, extensor of femur, FM, muscle of furca, IS, inner sternal; IT, inner tergal, LD, longitudinal dorsal muscle to head, LOS, lateral outer sternal; LT, lateral thoracic, LTG, longitudinal tergal, MC, muscles of cercus MOS, median outer sternal, MP, muscles of paramere, MR, muscles of reproductive system, OT, oblique tergal, PS, prosternal muscle, PT, 1st and 2nd pleurotergal muscles to head; SP, sterno-pleural, 1 TS, 1ry tergo-sternal; 2 TS, 2ry tergo-sternal, TSN transverse sternal, VL, ventral longitudinal muscle to head.

The musculature of the labium is similar to that of the maxilla. Arising from the posterior tentorial arms are the proximal (PRM) and distal (DRM) retractors of the mentum The proximals are inserted on the lateral basal angles of the mentum, and the distals on the anterior wall of the prementum at the inner basal angles of the glossae. As in *Dissosteira carolina* described by Snodgrass (1928), the glossae, paraglossae and palpi are all supplied with individual intrinsic muscles. Overlying the distal retractor muscle of the mentum is the retractor of the hypopharynx (RH), which is inserted on the posterior part of the hypopharynx. The buccal region and pharynx are supplied with dorsal, ventral and lateral dilator muscles (DP).

THORAX. The head is connected to the thorax by dorsal (Fig 34, LD) and ventral (Fig. 35, VL) longitudinal muscles, the dorsal extending from the post-occipital ridge to the posterior part of the pronotum and the ventral from the

posterior arm of the tentorium to the prosternum Also connecting the head to the thorax are the protergal (Fig 34, PT) and prosternal (Fig 35, PS) muscles extending from the postocciput to the pronotum and prosternum (Fig. 34).

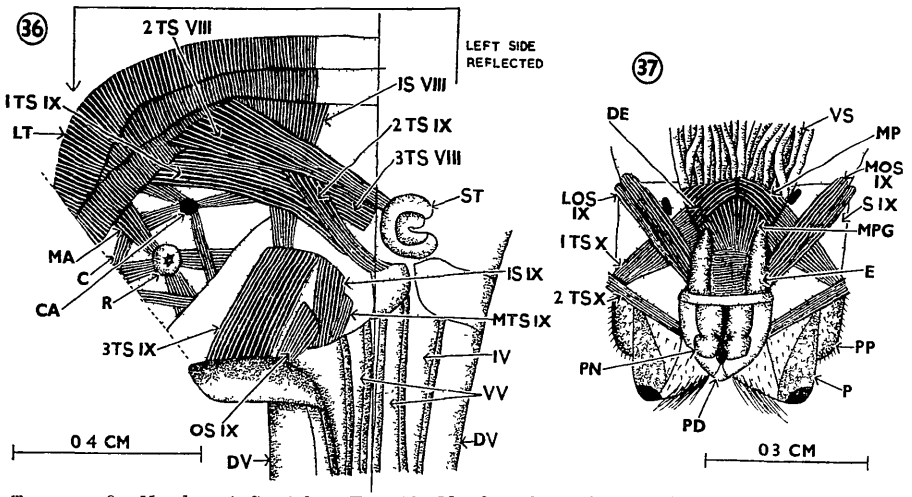
In the thorax longitudinal tergal (Fig. 34, LT), inner tergal (Fig. 34, IT), and sternal (Fig 35, IS) muscles occur in each segment and transverse sternal (Fig. 35, TSN) muscles are present in the meso- and metathorax where they act as retractors of the thorax The principal muscles of the thorax are those concerned with movement of the legs Since *M filifer* has no wings, the powerful muscles connected with flight are absent. There are three main muscles to each leg, the adductor (Figs. 34, 35, ADC) and abductor (Figs 34, 35, ABC) of the coxa, and the extensor of the femur (Figs 34, 35, EF) These arise on the sternum of their respective segment, the coxal muscles being inserted on the rim of the base of the coxa, and the femoral passing on to the femur

LEG Fig 40 In addition to those muscles in the thorax concerned with the movements of the leg as a whole, there are also a number of muscles within each joint of the leg The trochanter is operated by two muscles, the levator (LT) and depressor (DT) of the trochanter, arising on the base of the coxa and inserted on the rim of the trochanter In the femur the posterior levator of the tibia (PLT) occupies most of the cavity of the femur. The fibres of this muscle extend into the dorsal crest of the femur, while distally they taper to a thick stalk rising from the dorsal margin of the base of the tibia From the base of this stalk a short muscle extends dorsally in the distal part of the femur The anterior levator of the tibia (ALT) is represented by only a thin strand arising from the base of the tibia The depressor of the tibia (DTB) is a long slender muscle arising in the ventral part of the femur and tapering to its insertion on a long apodeme that arises from the knee joint A small muscle arising on the dorsal wall of the femur is inserted on the apodeme of the depressor of the tibia near its base The levator (LTA) and depressor (DTA) of the tarsus are two small muscles, the depressor longer than the levator, which arise on the distal part of the tibia and are inserted on the base of the tarsus The depressor of the pretarsus (DPT) consists of two small muscles, one arising in the proximal end of the tibia and the other on the ventral wall of the basal half of the tibia They are both inserted on a long tendon-like apodeme (TAD) arising from the unguitractor plate at the base of the claws

ABDOMEN In *Macropathus filifer* each segment of the abdomen appears to conform to a similar pattern. The muscles can be divided into longitudinal, dorsoventral and pleural.

Longitudinal muscles, which are divided into tergal (Fig 34, LTG) and sternal (Fig 35, IS) muscles, arise at the anterior margin of each segment, and are inserted into the anterior margin of the segment behind The tergal muscles form an almost continuous band over the surface of the terga, which is broken by a narrow gap medianly, where the heart runs the whole length of the thorax and abdomen Eleven pairs of alary muscles (Fig 41, AM) arise from the terga and spread out fanwise over the surface of the dorsal diaphragm The sternal muscles consist of two narrow bands connected anteriorly in each segment by a transverse sternal (Fig 35, TSN) muscle Segmentally, just internal to each longitudinal sternal muscle (Fig 35, IS) arise two small outer sternal muscles, a narrow oblique lateral (Fig. 35, LOS), and a small fan-shaped median (Fig 35, MOS) muscle which originate midway on the eusternite of their own seg-

ment and are inserted on the anterior margin of the following eusternite, thus connecting together the adjacent edges of the sterna. The longitudinal muscles function as retractors of the abdomen, and the tergals and sternals working together telescope the abdomen.



TEXT-FIG. 8 *Muscles of Genitalia*.—FIG 36—Muscles of female genitalia. FIG 37—Muscles of male genitalia.

CA, cercal aperture C cercal muscles DV dorsal valve DE, ductus ejaculatorius, E, endapophysis, IS VIII IS IX, inner sternal VIII, IX, LOS, lateral outer sternal IX, LT, longitudinal tergal, MA, muscle of anus, MOS, median outer sternal IX, MP, minor protractor muscle of genitalia, MPG, major protractor muscle of genitalia MTS minor tergo-sternal IX OS IX, outer sternal IX, P, parameie, PP, paraproct PN penis PD pseudosternite, R, rectum, ST, spermatheca deflected to left, S IX, sternite IX, 2TS VIII, secondary tergo-sternal VIII, 3TS VIII, tertiary tergo-sternal VIII, 1TS IX, primary tergo-sternal IX 2TS IX, secondary tergo-sternal IX, 3TS IX tertiary tergo-sternal IX 1TS primary tergo-sternal X, 2TS, secondary tergo-sternal X, VS, vesiculae seminales, VV, ventral valve

Dorso-ventral muscles, Figs. 34, 35, consist of primary (1TS) and secondary (2TS) tergo-sternal muscles. They arise from the tergum in each segment both segmentally and intersegmentally and are inserted on the sternum They are concerned with the mechanics of respiration.

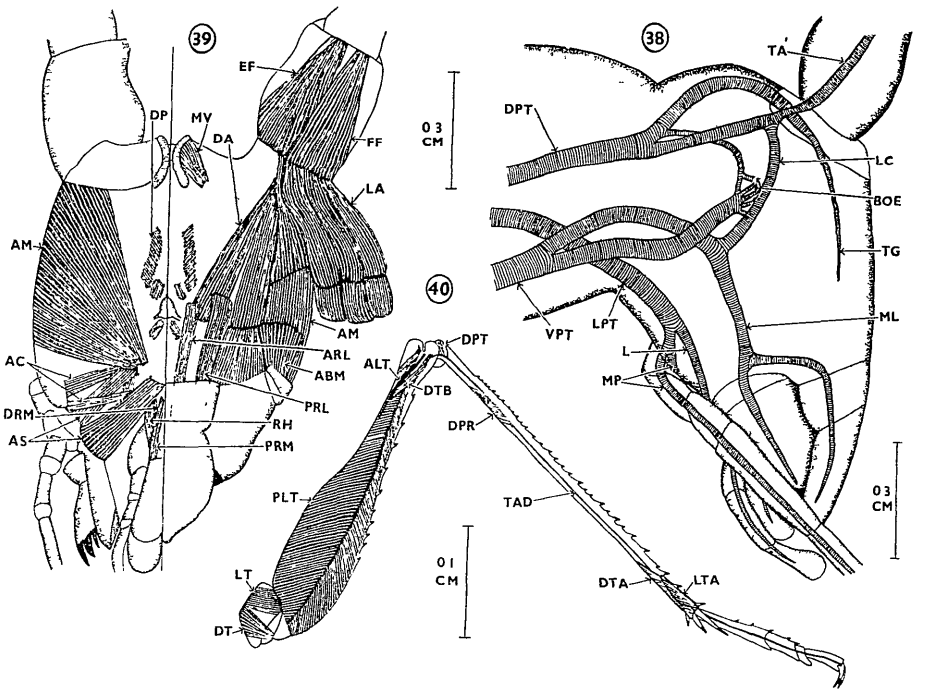
Pleural muscles in most insects can be divided into sterno-pleural and noto-pleural, but in *M. filifer* these do not occur.

The musculature of each spiracle consists of a short dorsal muscle for closing and a long ventral muscle for opening the spiracle

Musculature of Genitalia In segments VIII, IX, and X the muscles are modied for movement of the cerci and genitalia

Male Fig 37. In the male the musculature of segment VIII conforms with that of the preceding abdominal segments, but segments IX and X have undergone various changes Three tergo-sternal groups arise on tergum X The primary group (1TS X) is inserted on the endapophysis (E) of the ramus, the secondary group (2TS) on the pseudosternite and the tertiary group on the paraproct The outer sternal (OS IX) arises antero-laterally on sternum IX as in a typical segment and is divided into two groups—the lateral group (LOS) is inserted on the ramus, the medial (MOS) on the pseudosternite Thus the pseudosternite is controlled by both tergo-sternal and sternal muscles Arising on the pseudosternite and inserted on the ramus is the ramo-pseudosternal muscle The parameres are controlled by two muscles, the parameral muscle arises from the

pseudosternite and is inserted on the paramere, while a transverse parameral muscle acts between the two parameres. The ductus ejaculatorius is covered by two muscular sheets, the major (MPG) and minor (MP) protractor muscles of the genitalia, the major lying within the minor. The contraction of these two



TEXT-FIG. 9 *Trachea and Muscles of Head Muscles of Leg* FIG. 38—Lateral view head showing trachea passing to head capsule and mouth parts FIG. 39—Anterior view of head showing muscles On left deeper muscles of maxilla, hypopharynx and labium. On right muscles of labium, mandible and antenna FIG. 40—Muscles of hind leg

ABM, abductor of mandible AC, adductors of cardo, ALT, anterior levator of tibia, AM, adductor of mandible, ARL anterior retractor of labium, AS adductor muscle of stipes, BOE, branches to brain oesophagus and eye, DA, depressor of antenna DP, dilator muscles of pharynx, DPR, depressor of pretarsus DPT, dorsal prothoracic trunk DRM, distal retractor of mentum DT, depressor of trochanter, DTA, depressor of tarsus, DTB depressor of tibia, EF extensor of flagellum, FF, flexor of flagellum, L branch to labium LA, levator of antenna, LC, lateral connective; LPT, lateral prothoracic trunk LT, levator of trochanter, LTA levator of tarsus, ML, branch to mandible and labium, MP, branch to maxilla and palp, MV, muscle of vertex, PLT, posterior levator of tibia PRL posterior retractor of labium, PRM proximal retractor of mentum; RH, retractor of hypopharynx TA, trachea to antenna, TAD, tendon-like apodeme, TG, trachea to gena, VPT, ventral prothoracic trunk

muscles everts the genitalia. The cerci belong to the eleventh abdominal segment and are controlled by abductor, depressor and levator muscles (Fig 36, C) arising on tergum X.

Female. Fig. 36 In the female the muscles of segment VIII have been adapted to assist in the movement of the external genitalia. The inner sternal muscle (IS VIII) arises on the subgenital plate and is inserted on the interior intervalvula The tergo-sternal muscles are divided into three groups The primary one (ITS IX) is inserted on the subgenital plate, while the secondary has its origin on Tergum VIII (2TS VIII) and the tertiary (3TS VIII) arises on the intertergal apodeme on tergum IX; both are inserted on the basivalvula. In segment IX the inner sternal muscle (IS IX) arises on the second valvifer and is inserted on the paraproct The outer sternal (OS IX) arises on the median

apodeme of the superior intervalvula and is inserted on the second valvifer. As in segment VIII there are three tergo-sternal muscles The primary one (ITS IX) arises antero-laterally on tergum IX, the secondary group (2TS IX) lies just posterior to the primary group, the tertiary (3TS IX) arises laterally on the tergum, and they are inserted respectively on the inferior intervalvula, the inferior and superior apophyses. The muscles of the cerci (C) are as already described for the male.

Respiratory System

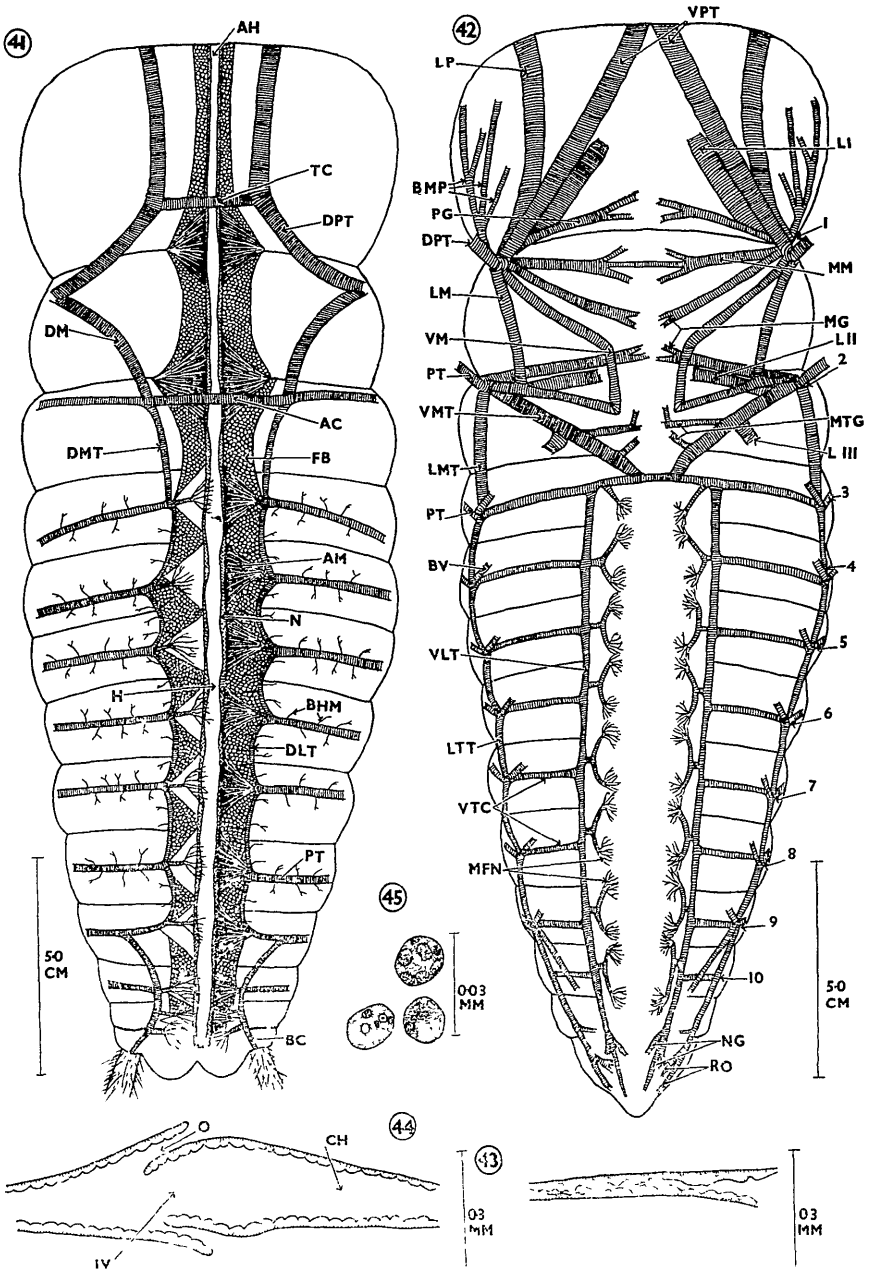
Respiration in *M. filifer* is of the primitive holopneustic type. The trachea open to the exterior by ten pairs of spiracles, two in the thorax and eight in the abdomen, all of which are situated in the pleura When filled with air, in a freshly killed specimen, the tracheae have a silvery appearance and can easily be traced down to the finest tracheoles

The main pattern of the trachea in *M filifer* consists of two dorsal longitudinal trunks (Fig 41, DLT) and two ventral longitudinal trunks (Fig 42, VLT) connected to two lateral tracheal trunks (Fig 42, LTT) by ventral transverse connectives (Fig 42. VTC) Unlike *Periplaneta,* there are no transverse connectives joining the two dorsal longitudinal trunks and the two ventral longitudinal trunks, except in the first abdominal segment where the ventral trunks are joined, and in the metathoracic segment where the two dorsal trunks are joined (Fig 41, AC)

Prothorax and Head These are supplied by tracheae from the first or mesothoracic pair of spiracles Each spiracle gives off three main trunks—a dorsal (Figs. 38, 41, DPT), a lateral (Fig 42, LP) and a ventral (Figs 38, 42, VPT) prothoracic trunk which all pass anteriorly into the head Besides these trunks the following branches are given off from the spiracles— a small branch divides into several smaller branches to supply the muscles of the prothorax (Fig. 42 BMP), another branch passes to the first thoracic ganglion (Fig 42, PG) and a large branch enters the fore leg (Fig 42 LI) The two dorsal longitudinal trunks are joined by a connective (Fig 41, TC) above the heart in the posterior part of the prothorax

Within the head (Fig 38) each trunk divides into several branches The dorsal trunk sends off three branches; one to the vertex and gena (TG), one to the antenna (TA) and one to the brain, compound eye and oesophagus (BOE) The branch to the antenna sends a lateral connective (LC) down to join a branch from the ventral trunk The ventral trunk splits into two main branches One passes up to join the branch from the dorsal trunk supplying the brain, compound eye and oesophagus and divides into several smaller tracheae The other branch divides into two—one linking with the dorsal trunk by the lateral connective and the other passing antero-ventrally to the labrum and mandible (ML). The lateral trunk passes ventrally and divides, one branch going to the maxilla (MP) and the other to the labium (L)

Mesothorax. This is supplied with tracheae from both the mesothoracic and metathoracic spiracles As in the prothorax, there are three main trunks which also originate from the mesothoracic spiracle Each dorsal longitudinal trunk in the mesothorax (Fig 41. DM) passes posteriorly to the junction with the palisade trachea (Fig 42, PT) in the anterior part of the metathorax, the ventral mesothoracic trunk (Fig 42. VM) passes posteriorly to join a lateral branch from the metathoracic spiracle in the anterior part of the metathorax; the lateral



TEXT-FIG 10 *Respiratory and Circulatory Systems*.—FIG. 41.—Dorsal view thorax and abdomen showing trachea, dorsal vessel and alary muscles. FIG. 42.—Ventral view thorax and abdomen showing trachea. FIG. 43.—Portion of aorta enlarged. FIG. 44.—Part of heart showing an ostium connecting two chambers. FIG. 45.—Blood corpuscles.

AC, abdominal connective; AH, aorta to head; AM, alary muscle; BC, branch to cercus; BHM, segmental branches to heart and dorsal muscles; BMP, branches to muscles of prothorax; BV, tracheal branches to viscera; CH, chamber of heart; DLT, dorsal longitudinal trunk in abdomen; DM, dorsal longitudinal trunk in mesothorax; DMT, dorsal longitudinal trunk in metathorax; DPT, dorsal prothoracic trunk; FB, fat body; H, heart; IV, interventricular passage; LI, trachea to first leg; LII, trachea to second leg; LIII, trachea to third leg; LM, lateral mesothoracic trunk; LMT, lateral metathoracic trunk; LP, lateral prothoracic trunk; LTT, lateral tracheal trunk; MFN, branches to abdominal muscles, fat body and nervous system; MG, trachea to mesothoracic ganglion; MM, branches to mesothoracic muscle; MTG, trachea to metathoracic ganglion; N, nephrocytes; NG, branches to nerve ganglion; O, ostium; PG, trachea to prothoracic ganglion; PT, palisade trachea to dorsal longitudinal trunk; RO, branches to reproductive organs; TC, thoracic connective; VLT, ventral longitudinal trunk; VM, ventral mesothoracic trunk; VMT, ventral metathoracic trunk; VPT, ventral prothoracic trunk; VTC, ventral transverse commissures.

mesothoracic trunk (Fig. 42, LM) connects the mesothoracic and metathoracic spiracles. From the mesothoracic spiracle a branch passes to the mesothoracic muscle (Fig. 42, MM) and another goes to the second thoracic ganglion (Fig 42, MG) which is also supplied by a branch from the metathoracic spiracle A branch from the metathorax passes anteriorly to supply the middle leg (Fig 42, LII).

METATHORAX. Branches from the metathoracic spiracle supply the metathorax. A lateral metathoracic trunk (Fig 42, LMT) connects the metathoracic spiracle with the first abdominal spiracle. The ventral metathoracic trunk (Fig 42, VMT) fuses with the ventral transverse commissure of the first abdominal spiracle and gives off branches to the third thoracic ganglion (Fig. 42, MTG) and a branch to the hind leg (Fig. 42, LIII). Each dorsal longitudinal trunk (Fig. 41, DMT) in the metathorax is connected medianly by the abdominal connective (Fig. 41, AC) and laterally each is joined to the metathoracic spiracles by a palisade trachea (Fig 41, PT).

ABDOMEN The eight pairs of abdominal spiracles are connected on each side by a lateral tracheal trunk (Fig. 42, LTT) From each spiracle four branches are given off—a lateral trunk (Fig 42, LTT), a dorsal palisade trachea (Fig 41, PT), a visceral branch (Fig 42, BV) and a ventral transverse commissure (Fig 42, VTC). The segmental palisade tracheae connect the two dorsal longitudinal trunks from the metathorax with the lateral tracheal trunks; the dorsal longitudinal trunks give off segmental branches which pass to the heart and dorsal musculature (Fig. 41. BHM) The visceral tracheae pass to the alimentary canal. The segmental ventral transverse commissures link the lateral tracheal trunks with the ventral longitudinal trunks, which give off segmental branches supplying the nerve cord, ventral muscles and fat body (Fig 42, MFN). From spiracle eight a branch passes to the ovary in the female, or the testis and vesiculae seminales in the male, and posteriorly spiracle nine supplies the last three segments and their appendages The dorsal longitudinal trunk sends a branch to the cerci (Fig 41, BC), while both the ventral and lateral trunks supply the last abdominal nerve ganglion (Fig 42, NG) and the muscles of the external genitalia (Fig 42, RD)

CIRCULATORY SYSTEM

The circulatory system is of the open type, there being only a single closed organ, the dorsal vessel The greater part of the circulation of the blood takes place in the cavities of the body and its appendages, the blood occupying the spaces between the internal organs There are two such spaces in *Macropathus filifer,* the dorsal or pericardial sinus and the visceral sinus, which are separated by a thin, transparent membrane, the dorsal diaphragm. No trace of a ventral diaphragm has been seen in *M filifer*, so there is no perineural sinus Maskell (1927) records it as being present in the thorax, but absent from the abdomen, in *Hemideina* The ventral diaphragm is present in most Orthoptera, though often it is incomplete

Within the dorsal diaphragm lies the dorsal vessel or heart (Fig 41, H), which is maintained in position within the pericardial sinus by suspensory filaments attached to the abdominal terga, and also by the diaphragm itself The heart consists of a long delicate tube which extends the whole length of the abdomen and into the prothorax. Anteriorly it is continued as the aorta into

the head (Fig. 41, AH), where it discharges ventrally in front of the brain. This extension of the heart into the prothorax is a primitive condition and has also been recorded for *Periplaneta* and *Hemideina*. In most insects the heart is restricted to the abdomen, where it is variously shortened so that there are usually fewer chambers than abdominal segments, sometimes only one. The heart of *Periplaneta* is extremely primitive, being composed of thirteen chambers. In *Hemideina* it consists of eleven chambers marked off from each other by constrictions, and this also appears to be the case in *Macropathus*. Each chamber of the heart (Fig. 44, CH) has a pair of laterally placed ostia (Fig. 44, O), but the aorta (Fig. 43) has no chambers or ostia.

On either side of the heart, in each segment, is a pair of alary muscles (Fig. 41, AM) which spread out fanwise over the surface of the dorsal diaphragm. The number of muscles present varies in different groups of insects from twelve pairs in *Periplaneta* to two pairs in the larva of *Chironomus*. In *Macropathus*, as in *Hemideina*, there are eleven pairs, corresponding to the number of chambers present. Between the alary muscles, and extending the whole length of the dorsal vessel on either side, is a dense mass of fat body (Fig. 41, FB).

Within the pericardial sinus, on either side of the heart, is a linear chain of brown tissue, the pericardial cells or nephrocytes (Fig. 41, N), which, according to Wigglesworth (1947), absorb colloidal particles from the blood. Imms (1946), however, considers they have the property of storing up substances of an excretory nature.

Spreading over the dorsal diaphragm are the dorsal tracheae, some of which penetrate into the pericardial sinus.

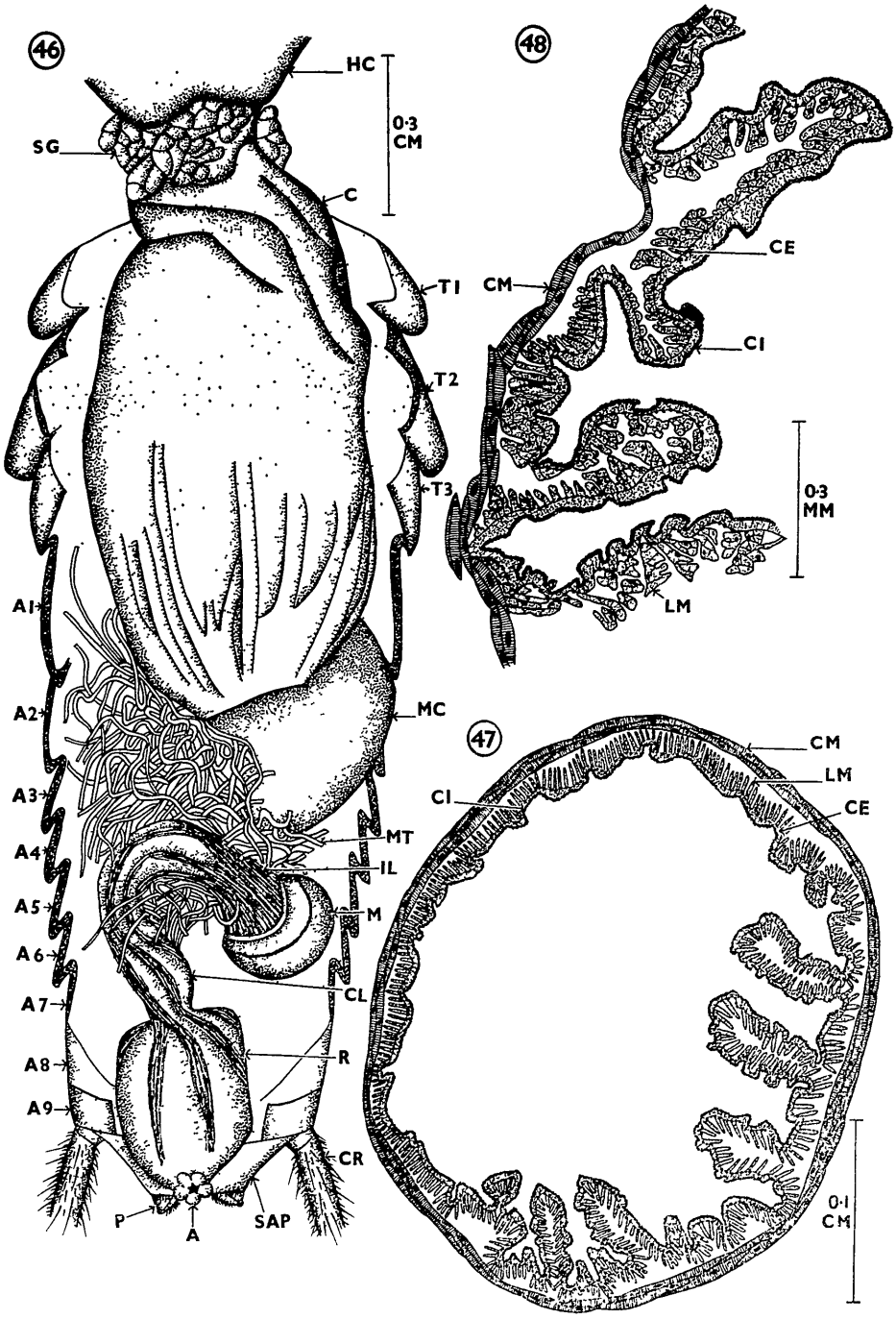
The heart is composed of a single layer of cells with large nuclei. It is subtended on either side by a thin structureless membrane. The inner surface of the cells is scolloped (Fig. 44). The blood is colourless and contains a large number of leucocytes (Fig. 45). These are circular with granular contents and probably function as phagocytes. Blood may easily be obtained from the visceral sinus of a freshly killed weta.

The Alimentary System

The alimentary canal of *Macropathus filifer* is approximately one and a-half times the length of the body. A typical example collected from Percy's Reserve shows this: Pharynx and oesophagus, 7 mm.; crop, 10 mm.; gizzard, 3 mm.; mesenteron, 10 mm.; ileum, 2 mm., colon, 10 mm., rectum, 4 mm.; total length, 46 mm.; length of body, 30 mm.

The alimentary canal is divided into stomodaeum, mesenteron (ventriculus) and proctodaeum. The stomodaeum and proctodaeum are lined with chitinous ectoderm and the mesenteron with endoderm.

Stomodaeum. A pair of salivary glands lie partly in the head and partly in the anterior part of the thorax, on each side of the crop. Each gland consists of a number of acini, which are each provided with a ductule. The ductules unite, forming a main duct on each side, and these two ducts unite into a single duct which opens to the exterior below the hypopharynx and above the labium. An elongate salivary reservoir opens into the main duct of each gland just anterior to their junction. The main ducts and their branches are provided with tracheoles, but the reservoirs are not. Sections through the acini (Fig. 50, GA) show the numerous nuclei and vacuolated cytoplasm of typical glandular tissue.

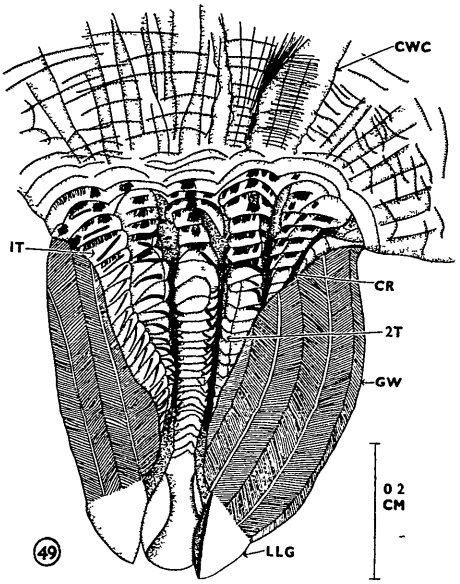


TEXT-FIG 11.—*Gut "in situ" and T.S. Crop* FIG. 46—Gut "in situ" FIG. 47—T.S. through crop FIG. 48—Portion of wall of crop enlarged

A, anus; A1, A2, A3, A4, A5, A6, A7, A8, A9, abdominal segments; C, crop; CE, chitin secreting epithelium; CI, chitinous intima; CL, colon; CM, circular muscle; CR, cercus; HC, head capsule; IL, ileum; LM, longitudinal muscle; M, mesenteron; MC, mesenteric caecum; MT, Malpighian tubules; P, paramere; R, rectum; SAP, supra-anal plate; SG, salivary gland; T1, T2, T3, thoracic segments.

The mouth is situated anterior to the base of the hypopharynx and immediately behind the base of the clypeus. The mouth leads into the oesophagus, a narrow muscular tube, which extends upward in the anterior part of the head, then turns to pass posteriorly beneath the brain but above the tentorium and leaves the head by the occipital foramen. The oesophagus swells out into the very large crop (Fig. 46, C) which fills the whole thorax and the anterior part of the abdomen. It is used for storage of food. It is capable of considerable distention, and when empty or partially full its wall is thrown into folds. The surface of the cuticular lining of the crop contains many ridges and folds which increase in intensity near the posterior end (Fig. 49). Sections of the crop show slight indentations on the dorsal surface and much stronger ones on the ventral surface (Fig. 47). The stronger indentations have serrated margins forming small teeth. The wall of the crop consists of a thick chitinous intima (Figs. 47, 48, CI) composed of two layers, an inner heavily staining layer (Fig. 53, IL) consisting of numerous fine indentations and chitinous setae, and a deeper, thicker stratified layer (Figs. 53, 54, OL). *Macropathus* differs from *Stenopelmatus* by having indentations in the inner layer of the intima, while that of *Stenopelmatus* is smooth. The stratified layer is irregular in thickness. Below this is the chitin secreting epithelium (Fig. 54, CSE) resting on a basement membrane with the cell walls not clearly defined. Outside the epithelium is a thick layer of striated longitudinal muscle (Figs. 47, 48, LM) and surrounding this is striated circular muscle (Figs. 47, 48, CM). At its posterior end the crop narrows and its chitinous intima increases in thickness and is thrown into six evenly distributed folds, which form the junction of the crop with the gizzard (Fig. 49). Within the gizzard these folds become raised into prominent ridges each bearing 27 large primary teeth (Fig. 49, 1T), making a total of one hundred and sixty-two. On either side of each row of primary teeth is a row of smaller secondary teeth (Fig. 49, 2T) making twelve rows in all, each row bearing twenty-one teeth. These are the "i lobi a spazzoli" of Berlese (1909) or "barbated lobes" of Du Porte (1918). At the base of the fold, between each pair of adjacent rows of secondary teeth, is a long, dark, heavily chitinous ridge (Fig. 49, CR) which bears no teeth Thus the full complement of proventricular teeth is four hundred and fourteen, of which one hundred and sixty-two are primary teeth and two hundred and fifty-two barbated lobes. This differs from *Stenopelmatus fuscus,* where there are two hundred and sixteen proventricular teeth, one hundred and thirty-eight being primary teeth and seventy-eight barbated lobes; and from *Hemideina thoracica,* where Maskell records one hundred and twenty primary teeth, but did not count barbated lobes. Internally the gizzard is constricted near its anterior end, the teeth on each ridge in this region being large, flattened apically and covered with yellow microtrichia (Fig. 52, MT). The clefts between them are very shallow. On each ridge, anterior to the constriction, are seven teeth which grow progressively smaller towards the crop They are rounded, slightly cup-shaped on the posterior margin and covered with stiff posteriorly directed microtrichia The most anterior "teeth" project into the crop and are mere projections of tissue tipped with chitin and bristles. In the region anterior to the constriction there are no barbated lobes or long chitinous ridges. Posterior to the constriction the teeth are large, triangular and yellow-brown in colour, with their apices posteriorly directed and sharply pointed with

dark brown chitin. These teeth become progressively smaller as they approach the mesenteron, the posterior two teeth being smoothly rounded with no chitinous points and the clefts between them very shallow. Both the chitinous ridge and the barbated lobes run from the eighth to the twenty-seventh primary teeth. The six folds pass posteriorly from the gizzard into the lumen of the mesenteron so that the posterior end of each forms one of the six flaps of the cardiac valve (Figs. 59, 60). Three of the flaps are large (Figs. 49, 59, LLG), curving

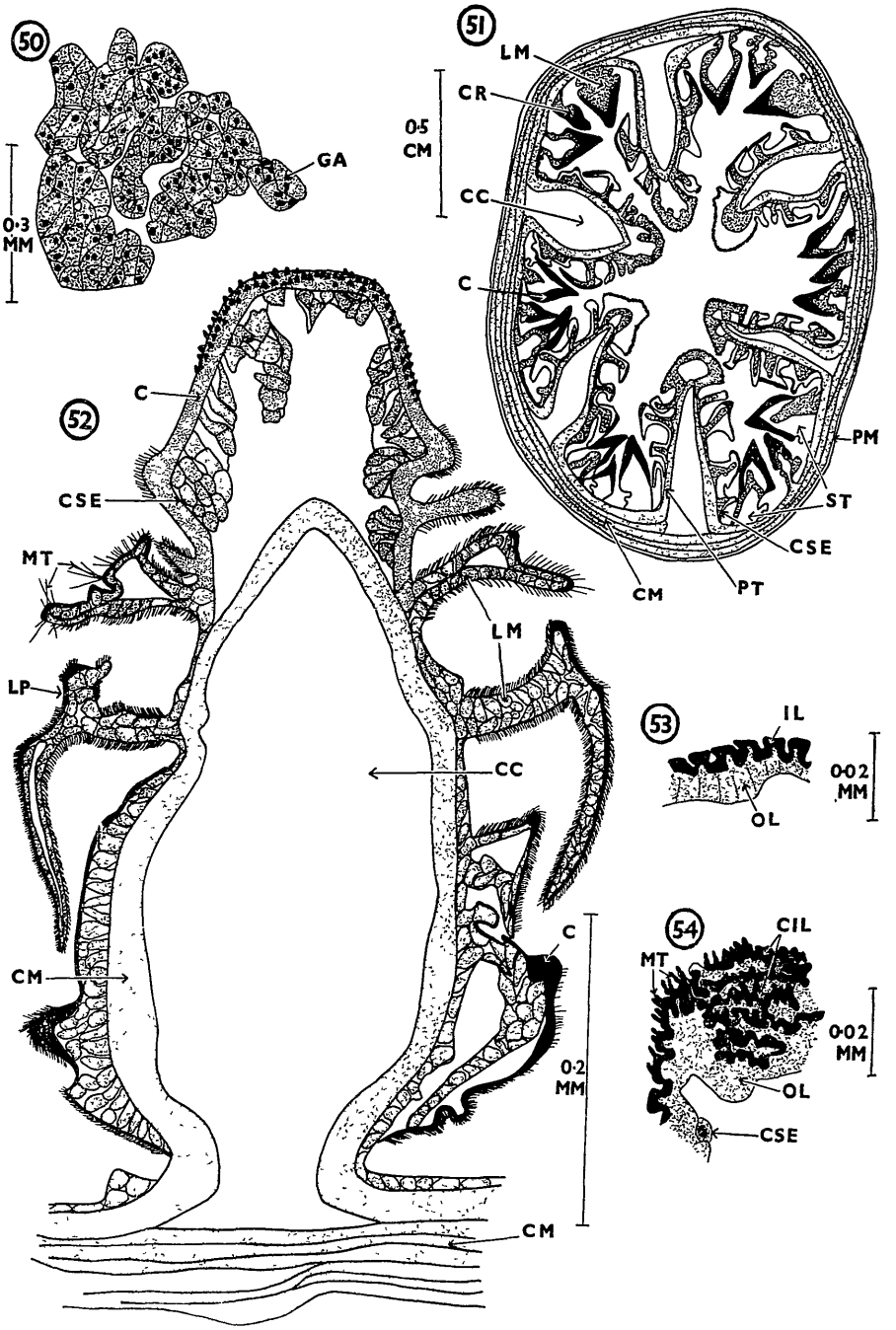


TEXT-FIG. 12. *Gizzard* FIG 49—Gizzard cut open to show teeth, and convolutions at junction of crop and gizzard

CR, chitinous ridge, CWC convoluted wall of crop; GW, gizzard wall, LLG, large lips of gizzard, 1T, primary teeth, 2T, barbated lobes

inwards to fit together, and form the main or primary section of the valve. Alternating with them are the other three shorter flaps (Fig. 59, SLG) which do not project as far into the mesenteron, but form a secondary basal section to the valve. In both fresh and preserved material they all appear a clear white. The valve acts as a filter, only allowing such food as is properly ground by the teeth to enter the mesenteron The structure of the valve in *Macropathus* differs from that described for *Hemideina* and *Stenopelmatus*. In all three insects there are six flaps, but in *Stenopelmatus* the two lateral flaps are longer than the other four, while in *Hemideina* there are two pairs of lateral folds and a dorsal and a ventral fold, each bearing a flap-valve.

The gizzard is composed of the same layers as the crop (Fig. 51) The chitinous layer is very thin between the teeth but thickens considerably over the teeth ridges, especially over the barbated lobes and the chitinous ridges Most of the surface of the chitin is produced into chitinous microtrichia. A thin layer of chitin-secreting epithelium (Figs. 51, 52, CSE) lies beneath the chitin Beneath the epithelium is a layer of connective tissue in which is embedded longitudinal muscle (Figs. 51, 52, LM) The primary teeth have three pairs of lateral projections (Fig. 52, LP) and the connective tissue and longitudinal muscle pass into each projection as well as into the apex of the tooth. They also line the barbated lobes and chitinous ridges. Lining each primary tooth, next to the longitudinal muscle, is a layer of circular muscle (Figs. 51, 52, CM). The rest of the tooth cavity is hollow (Fig. 52, CC). The circular muscle does



TEXT-FIG. 13. *T S. Crop, Gizzard and Salivary Gland.* (Scale in mm).—FIG. 50—T S salivary gland. FIG 51—T.S. gizzard. FIG. 52—Enlargement of primary tooth from gizzard showing lateral projections. FIG 53—Enlargement of chitinous intima of crop. FIG 54—Enlargement of chitinous intima of crop.

C, chitin; CC, central cavity, CIL, convolutions of inner layer of chitinous intima, CM, circular muscle, CR, chitinous ridge; CSE, chitin secreting epithelium, GA, glandular acinus, IL, inner layer of chitinous intima, LM, longitudinal muscle embedded in connective tissue, LP, lateral projection, MT, microtrichia; OL, outer layer of chitinous intima, PM, peritoneal membrane, PT, primary tooth; ST, barbated lobe.

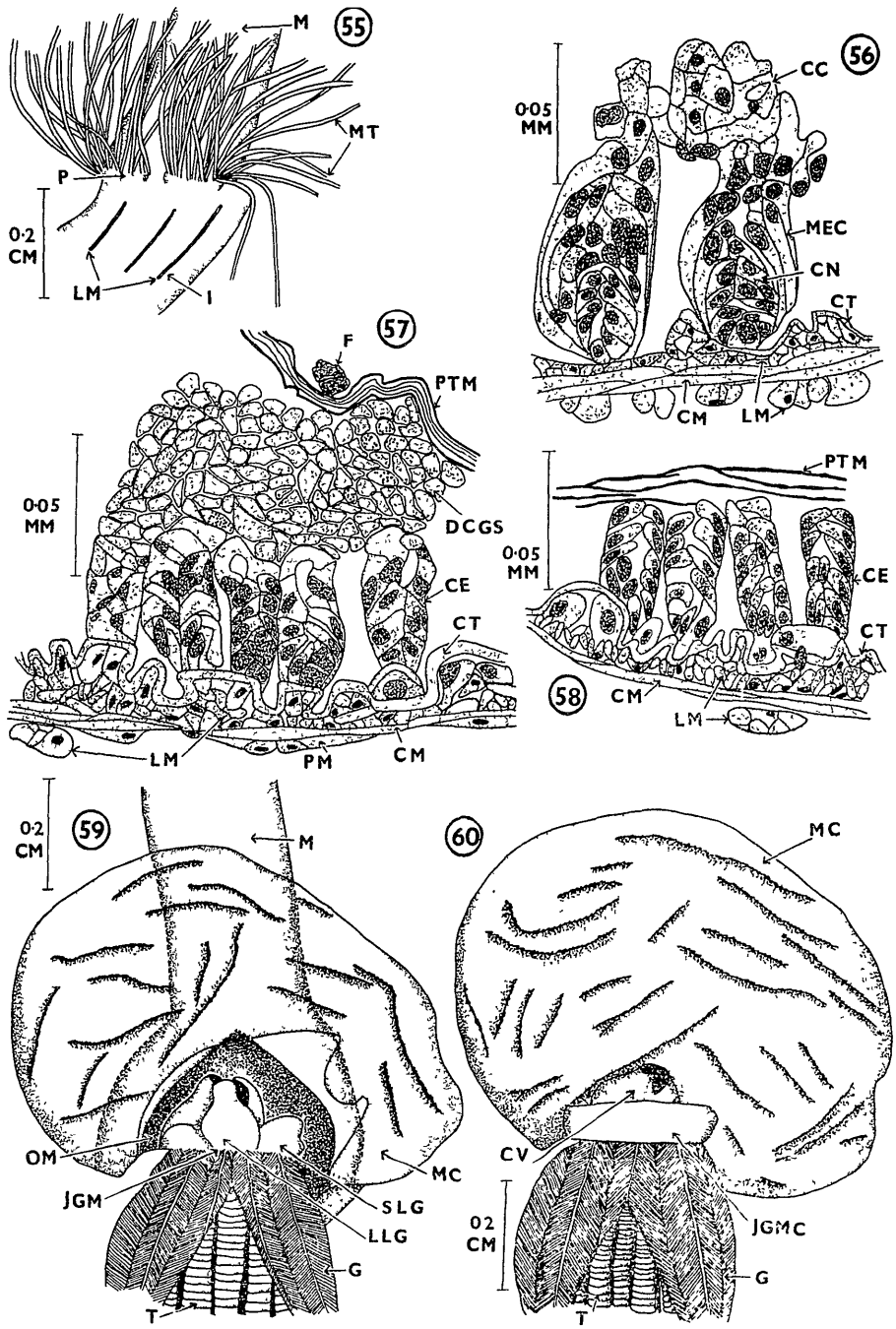
not project into the barbated lobes (Fig. 51, ST) or into the chitinous ridges (Fig. 51, CR). Surrounding the teeth ridges is a thick layer of unstriated circular muscle and outside this a conspicuous layer of peritoneum (Fig. 51, PM). The histological structure of *Macropathus* differs from *Stenopelmatus* and *Hemideina* in the possession of a large tooth cavity, longitudinal muscle being present in barbated lobes and chitinous ridges, and the circular muscle not being striated.

MESENTERON. The mid gut consists of the intestine proper and two forwardly directed projections from it, the mesenteric caecae (Figs 59, 60, MC), which completely enclose the gizzard, one being dorsal to it, and the other ventral The epithelial layer of each caecum has several deep folds in it, which serve to increase the secretory surface. The histological structure of intestine and caeca is similar (Figs 56, 57, 58)

The whole of the mesenteron (Figs 56, 57, 58) is covered with a thin layer of peritoneum. There are three muscle layers—a thin outer layer of scattered smooth longitudinal muscle fibres (LM) which are more numerous in the caeca than in the intestine proper, a middle thin layer of smooth circular muscle (CM), which differs from *Hemideina* where it is striated, and an inner layer of smooth longitudinal muscle This inner layer of longitudinal muscle is not present in *Hemideina* but does occur in *Stenopelmatus* *Stenopelmatus* differs from both *Hemideina* and *Macropathus* in having all the muscles of the mid gut striated. Within the muscular layer is a layer of connective tissue (CT) which, on its inner side, penetrates a little way between the epithelial cells forming thick basal walls or nests ("nidi") (CN).

The epithelium of the mid gut forms the greater part of the gut wall Within each of the nests formed by the connective tissue is a mass of cells, the lower ones of which are continually dividing to form new cells The nuclei are very crowded and flattened in the centre of the nest On each side of them, continuing up the nest walls, are the attenuated bases of the mature epithelial cells (MEC). As the cells are pushed outward and upward from the centre, they elongate and the nuclei become first round, then much elongated The outermost cells are fully mature and functional and should bear the striated hem which forms the lining of the intestine This striated hem, however, has never been observed in *Macropathus filifer*. The outermost cells of each nest eventually collapse during secretion and are lost, and the younger cells next to them are forced outward to fill the gaps Perfectly formed "nidi" are common in the caeca, but not so common in the intestine proper

Several peritrophic membranes (PTM) may be seen between the epithelium and the food contents Davis (1927) says, "The peritrophic membrane is an envelope of secreted substance that encloses the food material in the intestine of some insects It is elastic and non-cellular, so that it is not a true membrane". There has been much discussion as to the origin of the peritrophic membrane Van Gehuchten (1890), working with *Ptychoptera* larvae, thought it to be a product of special glandular cells at the anterior edge of the mesenteron and Cuenot (1898), Vignon (1899) and Bordas (1905) agree with this Thus the peritrophic membrane would be a single continuous chitinous tube, being continuously formed at the posterior end of the stomodaeum and passing out of the anus surrounding the faeces. Imms (1925) says, "The results of recent research indicate that the peritrophic membrane is continuously secreted by a band of



TEXT-FIG. 14 Mesenteron FIG 55—Malpighian tubules arising from two papillae at junction of mid and hind gut FIG 56—T S mesenteric caecum showing two "midi" FIG 57—T S mesenteron showing cast off digestive cells FIG. 58—T S mesenteron FIG. 59—Junction of fore and mid gut showing cardiac valve projecting into anterior part of mesenteron (Wall of mesenteric caecum reflected) FIG 60—Junction of fore and mid gut Mesenteric caecum overlying cardiac valve

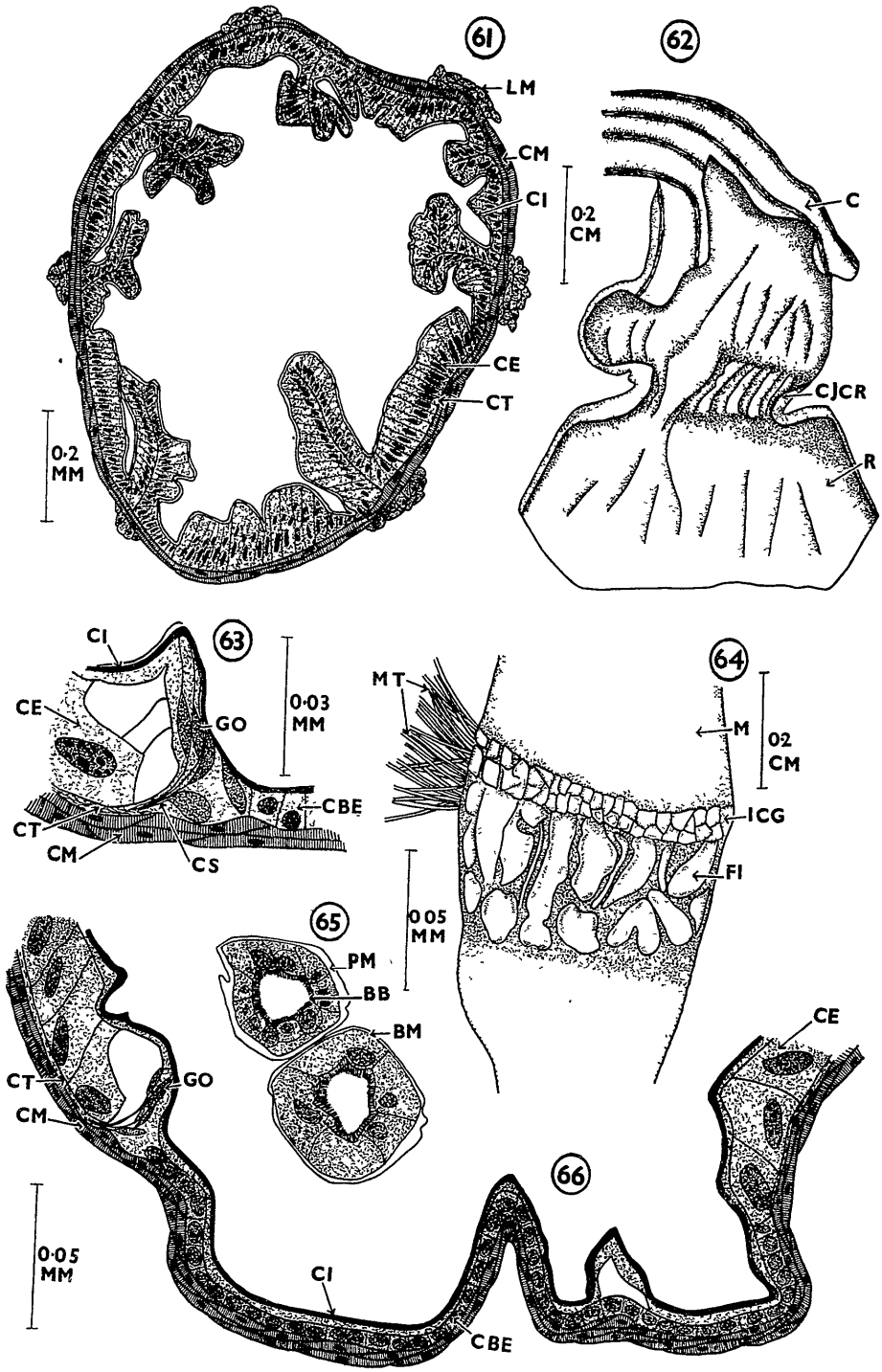
CC, cast off cell, CE, columnar epithelium CM circular muscle CN 'midus' or cell nest, CT, connective tissue, CV, cardiac valve DCGS cast off digestive cells and granules and globules of secretion, F, food, G, gizzard, I ileum JGM junction of gizzard and mesenteron, JGMC, junction of gizzard and mesenteric caecum LLG three large lips of gizzard LM longitudinal muscle, M, mesenteron, MC, mesenteric caecum, MEC, mature epithelial cell, MT, Malpighian tubules, OM opening to mesenteron, P papillae, PM, peritoneal membrane, PTM, peritrophic membrane, SLG two of three smaller lips of gizzard, T, teeth

deeply-staining gland-like cells situated at the point of junction of the fore and mid intestine". However, many authorities consider the membrane is a product of the epithelial cells of the mesenteron. Among these are Plateau (1877), Frenzel (1882, 1885), Balaiani (1890), Voinov (1898), Tillyard (1917) and Snodgrass (1925). In this case the membrane is non-chitinous and not necessarily continuous. Imms (1925) says, "The peritrophic membrane is described as being formed by the delamination of the inner or free margin of the cells lining the mid intestine". In the second case one could expect several peritrophic membranes overlapping, and this is what is found in *M. filifer*. The membrane appears to be formed at the surface of the epithelial cells. When the epithelium is actively secreting, the products of the cells (CC) containing granules and globules of digested secretion are extruded and forced under the membrane, thus tearing it free from the epithelial cells. These cells accumulate between the membrane and the epithelium, which is then regenerated from the nests of cells. The result of this is a series of very folded, wrinkled, incomplete peritrophic membranes, one inside the other.

At the junction of mesenteron and hind gut are two small papillae (Fig. 55, P) from the dorsal surfaces of which the Malpighian tubules (Fig. 55, MT) arise. These papillae (ureters) open into the ileo-caecal groove (Fig. 64, ICG). This differs from *Stenopelmatus* and *Hemideina* where there are six ureters at equidistant points round the gut. Each tubule (Fig. 65) is surrounded by peritoneum (PM). Within this is a single layer of large epithelial cells resting on a basement membrane (BM) and containing prominent nuclei. The cytoplasm of the cells possesses minute granules which are concretions or droplets. The number of cells present in each tubule varies, and the cell walls are not always distinct. The inner margins of these cells possess a brush border (BB) which appears to be made up of short non-vibratile cilia that project into the lumen. There has been much controversy over the structure of the border Wigglesworth (1947) says: "It may be accepted at the present time that this border can be of two kinds: (1) the type called 'honeycomb border' (Wabensaum), which appears to be made up of a great number of little rod-like vesicles fused together so as to form a rigid palisade, and (2) the type called 'brush border' (Bürstensaum), which consists of separate filaments quite independent of one another". Maskell (1927) records the honeycomb border as occurring in *Hemideina,* but the brush border has been described for *Stenopelmatus* and other members of this group. The lumen of each tube is irregularly circular and is often filled with crystals. There are over two hundred and fifty Malpighian tubules present in *M. filifer*

PROCTODAEUM

Ileum. The ileo-caecal groove (Fig. 64, ICG) is very distinct and forms the junction between mesenteron and proctodaeum. The ileum is short and its inner surface is thrown into six irregular folds (Fig. 64, FI) which project into the lumen. The wall of the ileum (Fig. 61) consists of a thin chitinous intima (CI) beneath which is a layer of columnar epithelium (CE) with oval nuclei. Connecting the epithelium to the muscle layers is a thin band of connective tissue (CT). These three layers are thrown into six irregularly-shaped longitudinal folds of greater or less size, which become prominent near the posterior end, and are capable of being extended. Between these are six longitudinal bands of



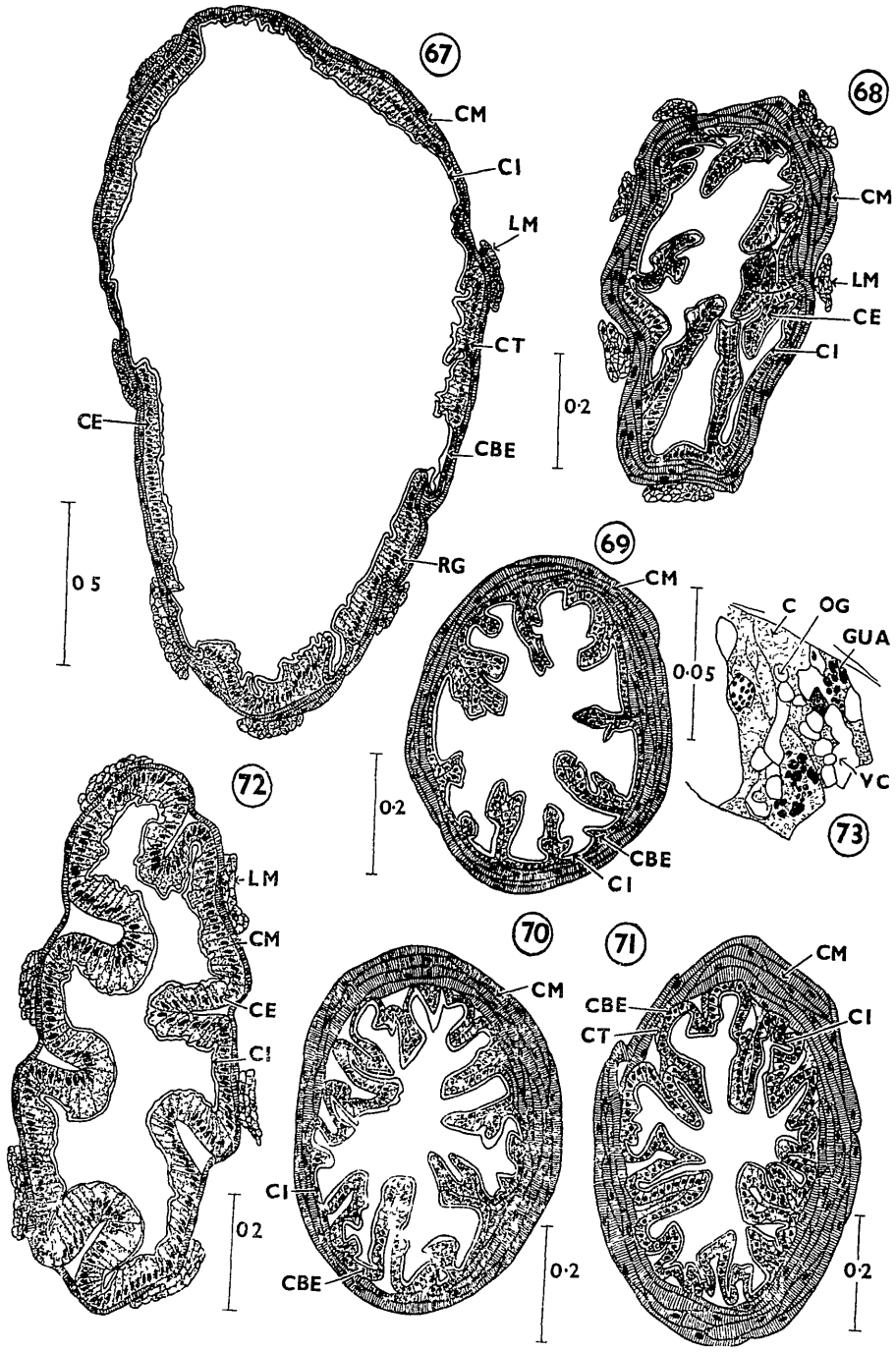
TEXT-FIG. 15 *T S Hind Gut* FIG. 61—T S Ileum FIG. 62—Junction colon and rectum—wall cut open and reflected to show constriction. FIG. 63—Enlargement of T.S. rectum showing "gland organ" FIG. 64—Junction mid and hind gut—internal showing ileo-caecal groove FIG 65—T S Malpighian tubules FIG 66—T.S rectum showing ends of two rectal glands, "gland organ and cuboidal epithelium linking two glands

BB, brush border, BM, basement membrane, C, colon, CBE, cuboidal epithelium, CE, columnar epithelium, CI, chitinous intima, CJCR, constriction at junction of colon and rectum, CM, circular muscle, CS, cytoplasmic strands, CT, connective tissue FI, folds of ileum, GO "gland organ", ICG ileo-caecal groove, LM, longitudinal muscle, M, mesenteron, MT Malpighian tubules, PM, peritoneal membrane, R, rectum.

columnar epithelium. There is a narrow band of striated circular muscle (CM) and surrounding this are six bands of striated longitudinal muscle (LM), which extend the full length of the hind gut. According to most authorities there is an inner layer of longitudinal muscle, but no trace of this has been seen in *M. filifer*.

Colon. Fig. 72. The colon is long and bent back upon itself. It consists of the same layers as the ileum. In the colon the six folds of the ileum are continued. Here they are large and of approximately equal size Between these folds are six longitudinal bands of columnar epithelium (CE). There is a very thin layer of striated circular muscle (CM) and outside this the six bundles of longitudinal muscle (LM) which correspond to the longitudinal bands of columnar epithelium. There is no internal longitudinal muscle.

Rectum. There is a marked constriction at the junction of colon and rectum (Fig. 62, CJCR). At the posterior end of the colon the epithelial folds become elongated and the epithelial layers between become narrower (Fig. 68). The striated circular muscle increases considerably in thickness so that it is capable of closing the aperture between colon and rectum At the termination of the colon the hind gut widens abruptly into the rectum. The chitinous intima (CI) is thin and, unlike *Hemideina,* of an even thickness throughout the rectum (Fig. 67). The epithelium is of two kinds, that of the rectal glands proper and that between them. The latter is much reduced, consisting of six narrow, corrugated strips of thin cuboidal epithelium (Figs. 66, 67, CBE) with small round nuclei. The presence of this cuboidal epithelium agrees with the statements of Maskell (1927) on *Hemideina* and Davis (1927) on *Stenopelmatus,* but differs from the results of Miall and Denny (1886) on *Periplaneta* and Cameron (1912) on *Bacillus rossi* where no epithelium is present beneath the corrugated intima Miall and Denny state that in these areas the chitinous lining blends with the basement membrane, while Cameron says that between each two bands is a non-epitheliated interspace, where the chitinous intima becomes corrugated and is closely applied to the basement membrane. There are six rectal glands (Fig. 67, RG) which are continuations of the six longitudinal bands of columnar epithelium (CE) of the colon The cell walls are distinct and the nuclei are oval The inner surface of the epithelium and the intima are thrown into ridges and folds. These rectal glands are similar to those of *Hemideina* and *Stenopelmatus.* According to Maskell they have no glandular structure but "agree with the description by Chun of rectal glands in *Locusta viridissima* (quoted by Packard, 1903) Minot has stated that Chun's description is applicable to the Acridiidae he has investigated, and he states that the rectal folds 'do not offer the least appearance of glandular structure' " Between the rectal gland and the cuboidal epithelium is a structure similar to that described by Davis (1927) as a "gland organ" (Figs. 63, 66, GO). There is a distinct gap between the two epithelia which contains from four to seven small, lens-shaped cells (GO), consisting of a large nucleus surrounded by a thin layer of cytoplasm. On the side towards the lumen, cytoplasmic strands (Fig. 63, CS) pass out from each cell and attach themselves singly to the chitinous intima (CI). No thin plate of non-staining chitin for the attachment of these strands such as Davis describes has been observed. Cytoplasmic strands also leave the other side of each cell, and these strands unite to form a cord which passes into the connective tissue This is markedly different from *Stenopelmatus* where each cell gives off only one thread Here the threads are twined into a cord passing towards the lumen. Davis says,



TEXT-FIG 16 *T S Hind Gut* (Scale in mm) —FIG. 67—T S rectum FIG. 68—T S junction colon and rectum FIG. 69—T S posterior end of rectum FIG 70—T S. mid anal region FIG 71—T S posterior anal region. FIG 72—T S colon FIG 73—T S fat body

C, cytoplasm, CBE, cuboidal epithelium, CE columnar epithelium CI chitinous intima, CM, circular muscle, CT connective tissue, GUA granules of uric acid, LM longitudinal muscle; OG, oil globule, RG, rectal gland, VC, vacuoles

"I am unable to explain the function of this peculiar structure . . . These organs may function as mucus-glands (although they do not resemble mucus-tissue in other animals), or they may draw off the excess water from the faeces. The latter would be a logical theory since the insect is an inhabitant of semi-arid country". As *Macropathus* lives under conditions of high humidity, and yet has a "gland" similar to that found in *Stenopelmatus,* it seems far more probable that the function of this "gland" is for secretion of mucus to assist in the expelling of faeces. The epithelium is joined to a thin layer of striated circular muscle (CM), about three fibres thick, by well developed connective tissue The six bands of longitudinal muscle (Fig. 67, LM) are present on the outer surface. The rectum narrows at its posterior end and passes into the anus. At their junction the rectal glands terminate abruptly and cuboidal epithelium (Fig. 69, CBE) is found in the anal region. The connective tissue (CT), epithelium (CBE) and intima (CI) are thrown into folds which gradually increase in size and number towards the anal aperture (Figs. 70, 71). The striated circular muscle (CM) is greatly thickened, but no longitudinal muscle occurs

Fat Body

The fat body (Fig. 73), a white opaque tissue, consists of a loose meshwork of lobes invested in delicate connective tissue, and is used for storage of reserve materials. It occurs throughout the body, but especially in the abdomen where it surrounds the gut and reproductive organs. It is a cellular tissue, but quite commonly the cell walls are not present.

Two types of cells are present in the fat body—trophocytes and urate cells The trophocytes which form the greater part of the fat body are characterised by strong vacuolation (VC) of the cytoplasm (C), which contains globules of oil-like fat (OG). The urate cells have very little fat, but instead contain small granules which are products of uric acid (GUA).

Imms (1931) says animals living in the dark in caves have an extra large amount of fat body, and this appears to be the case in *Macropathus filifer.*

Reproductive System

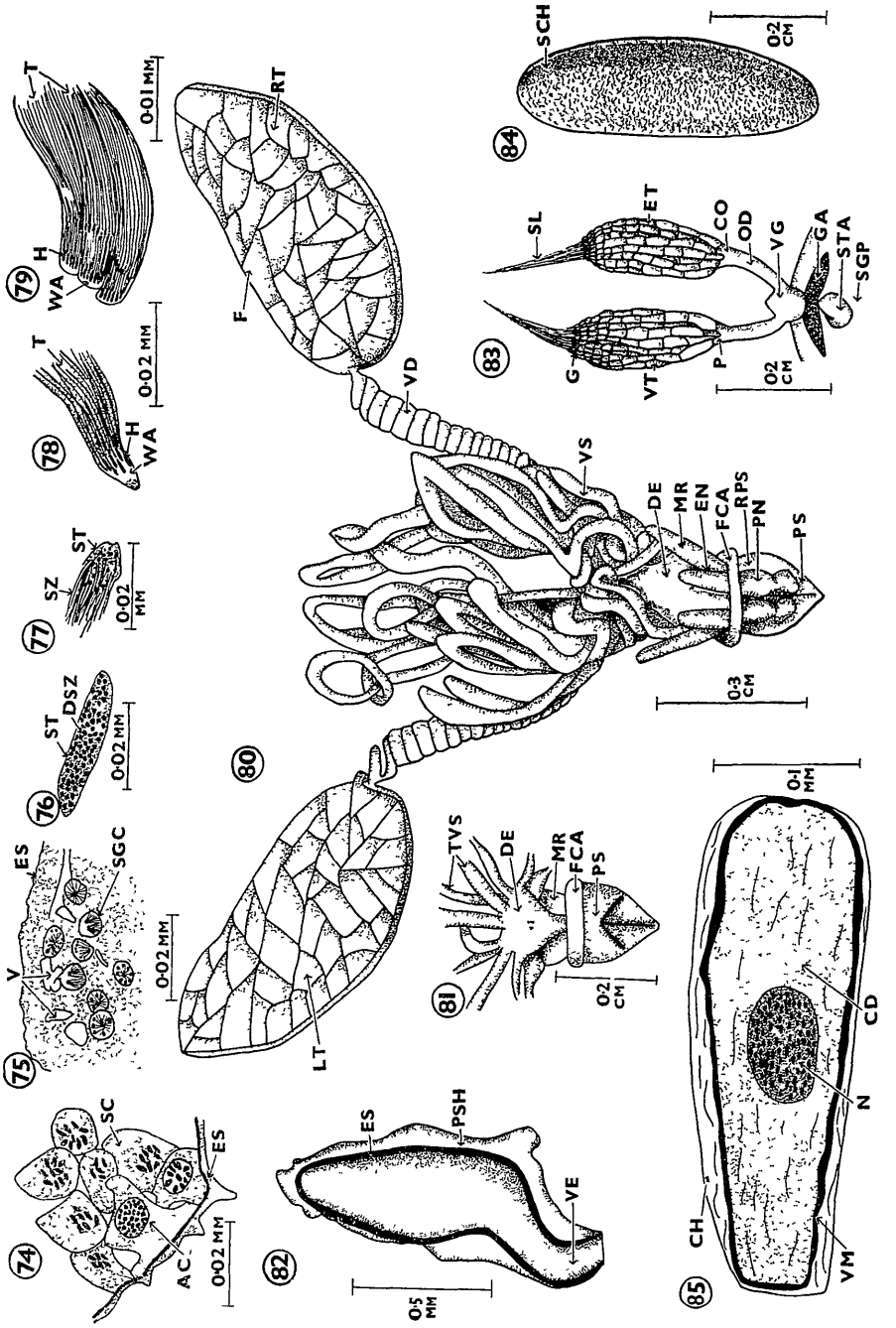
A. Female

Consists of two ovaries, two oviducts (Fig. 83, OD), a median vagina (Fig 83, VG) and a median spermatheca (Fig. 83, STA) for reception and storage of spermatozoa (Fig. 77, SZ) Each ovary is made up of from 24 to 26 ovarioles united at their anterior ends in a suspensory ligament (Fig 83, SL) There are usually twelve oöcytes in each ovariole which, along with the whole ovary, are covered by a thin structureless membrane, the tunica propria.

The terminal filament (Fig. 83, SL), an egg tube (Fig. 83, ET), and a supporting stalk or pedicel (Fig 83, P), as defined by Snodgrass (1935a) are all present in *Macropathus filifer.*

1. *The terminal filament* (SL) which forms the anterior part of the ovariole is slender and threadlike and consists of a solid strand of cells ensheathed in the tunica propria. The terminal filaments are united together to form the suspensory ligament.

2 *The egg tube* (ET), the middle and main portion of the ovariole, contains the germ cells. Each egg tube consists of two parts· the anterior end is the end chamber, or germarium (Fig 83, G), containing germ cells in an active state



TEXT-FIG 17.—Reproductive System. FIGS 74-79—Histology of testis showing development of spermatozoa. FIG. 74—Germarium. FIG 75—*Spermatogonial cells*. FIG 76—Spermatid containing developing sperms. FIG. 77—Spermatid ruptured to release sperms. FIG 78—Sperm bundle. FIG 79—Three sperm bundles grouped together. FIG 80—Dorsal view male reproductive system. FIG 81—Ventral view lower portion of male reproductive system. FIG 82—L.S. follicle of testis. FIG 83—Dorsal view female reproductive system. FIG 84—Mature egg. FIG 85—Oocyte from posterior end of ovary.

AC, apical cell; CD, cytoplasm and deutoplasm; CH, chorion; CO, calyx of oviduct; DE, ductus ejaculatorius; DSZ, developing spermatozoa; EN, endapophysis; ES, epithelial sheath; ET, egg tube; F, follicle; FCA, feebly chitinized arch connecting ramus; G, germarium; GA, genital aperture; H, heads; LT, left testis; MR, muscle attached to ramus; N, nucleus; P, pedicel; PN, penis; PS, pseudosternite; PSH, peritoneal sheath; RPS, ramus of pseudosternite; RT, right testis; SC, spermatogonia; SCH, chorion sculptured; SGC, spermatogonial cyst; SGP, subgenital plate; SL, terminal filaments uniting as the suspensory ligament; ST, spermatidia; STA, spermatheca; SZ, spermatozoa; T, tails; TVS, tubules of vesiculae seminales; V, vacuoles; VD, vas deferens; VE, vas efferens; VG, vagina; VM, vitelline membrane; VS, vesiculae seminales; VT, vitellarium; WA, white area.

of division and incipient differentiation, and behind this is the zone of growth, or vitellarium (Fig. 83, VT), the region in which the egg cells grow and attain their mature size. From the germarium are differentiated the oöcytes (Fig. 85) and the follicular epithelium which forms the egg chamber for each oöcyte, and also secretes on its inner surface the egg shell or chorion (SCH) The outer surface of the chorion retains the marks of the cells that produced it in the form of a honeycomb pattern of fine ridges reproducing the outlines of the cells of the follicular wall (Fig. 84). At the upper end of the egg the chorion is incomplete, and this part forms the micropyle of the egg. Since oocytes are produced continuously from oögonia, the first encysted oocyte becomes the lowermost and the first mature oöcyte in the vitellarium. Thus the region contains a linear series of oocytes gradually increasing in size as they near the oviduct Maturation of the oöcyte does not take place until the egg is laid, even though it is encased in the chorion which is tough, strong and white in colour.

There are two principal types of egg tubes in insects distinguished by the presence or absence of special nutritive cells within the follicular tubes Those with cells specialized to provide nutrition for the ova are meroistic and those without are panoistic. In *Macropathus filifer,* and most Orthoptera, there are no nutritive cells present and the egg tubes therefore belong to the panoistic type

3 *The pedicels* (Fig 83, P) of the ovarioles are short ducts connecting the egg tubes with each lateral oviduct (Fig 83, OD) When the first egg is ready to be laid the wall of the pedicel is dissolved away and the egg passes down into the oviduct The upper part of the oviduct, the egg calyx (Fig 83, CO), can become greatly dilated and serves as a pouch for storing some of the eggs till they are laid The oviducts are simple muscular tubes without accessory structures of any kind The complete structure of the ovaries may be seen only in an immature female of *Macropathus filifer.* In a gravid female the most distal eggs have matured and severed the connection of the pedicels to the calyx of the oviduct Most of the eggs lie loose in the body cavity on either side of the hind gut and when required pass to the calyx of the oviduct and from there to the exterior.

The two oviducts unite to form a short median vagina (Fig. 83, VG) opening on the under surface of the sub-genital plate (Fig. 83, SGP) which forms the roof of the copulatory chamber The vaginal aperture may be closed by a little flap of tissue attached to the base of the sub-genital plate

The spermatheca (Fig. 83, STA) consists of a median blind tube with muscular walls, branching half way along its length into two tubes the longer of which curves over the shorter one. Unlike the spermatheca of most insects, it does not open into the vagina but on to the lower surface of the copulatory chamber. It seems probable that during copulation the flap of tissue at the entrance to the vagina can be pressed over the aperture, closing it so that the spermatozoa, being unable to pass up that way, go to the spermatheca for storage. Fertilization of the egg must take place as it crosses the copulatory chamber and passes the spermathecal aperture, on its way to the valves of the ovipositor and the exterior

MALE

Two large, white, kidney-shaped bodies, the testes (Fig 80, LT, RT), lie in the abdomen on either side of the hind gut Each testis is made up of

numerous elongate sperm tubes or follicles (Figs 80, 82, F) which are arranged round the periphery and taper inwards. Each sperm tube is surrounded by a thin layer of peritoneum (Fig 82, PSH) which serves to bind the testis together into a compact structure The sperm tube wall consists of a thick vacuolated epithelial sheath (Fig 82, ES) According to Snodgrass (1935a) sperm tubes do not have a true follicular epithelium such as that which forms the walls of egg chambers in the ovary. This has been verified in *Macropathus filifer*.

As in the female egg tube each sperm tube consists of a germarium containing apical cells (Fig 74, AC) and spermatogonia (Fig 74, SC), a zone of growth containing spermatocysts (Fig. 75, SGC), a maturation zone containing spermatids (Fig 76, ST) and a zone of transformation containing spermatozoa (Fig. 77, SZ).

The germarium consists of an apical cell surrounded by spermatogonia (Fig. 74). The large apical cell (AC) is believed to be the primary spermatogonium of the tube which through division gives rise to all the other spermatogonia.

Encysted spermatogonia (Fig. 75, SGC) are present in large numbers in the zone of growth The origin of the male cyst cells in insects is not definitely known, but, while some investigators have believed that these cells are derived from the sheath of the sperm tube, most writers consider them as products of the germ cells. According to Miall and Denny (1886) spermatocysts are peculiar to Insects and Amphibia Berlese (1909) considers the cyst or nurse-cells and germinative cells (spermatogonia) are differentiated at the blind end of the testicular lobule. Then a number of nurse-cells form a cyst round a number of spermatogonia. Berlese has summarised the views of investigators of his day. "By Sutten (1900) and Voinov the cyst cell is compared to a primary spermatogonium, by Holmgren to an indifferent syncytium, by Paulmier (1899) and Gross (1904) to connective elements. Korschelt and Heider (1902) derive it from an indifferent initial cell Finally Henneguy (1904) considers that the cyst cell ought to be homologised with the ovarian epithelial cell."

According to most writers the spermatocysts enlarge and undergo spermatogenesis until finally near the vas efferens (Fig 82, VE) they contain spermatids (Figs. 76, 77, ST) and spermatozoa (Figs. 77, 78, 79, SZ) Maskell (1927) says that in the sperm tube of *Hemideina thoracica* the spermatozoa are free from one another within the cyst wall, but are found in bundles in the vasa deferentia (Fig 80, VD) free from the cyst. In *Macropathus filifer*, however, mature spermatozoa in bundles are found free scattered throughout the whole sperm tube and are not confined to the end nearest the efferent duct Sometimes the bundles are solitary (Fig. 78) but more frequently several bundles are grouped together (Fig 79).

With the elongation of the spermatocyst the nuclei within multiply, and pass into the spermatid stage (Fig. 76). The nuclei form the heads of the developing spermatozoa and when they are fully formed the cyst wall ruptures and the sperms are set free (Fig 77) The spermatozoon consists of three parts—anteriorly a head (Fig. 78, H), then a short middle portion, and posteriorly a very long tail (Fig. 78, T). The sperm bundle consists of three parts also—anteriorly there is a white area (Figs 78 79, WA) which curves back postero-laterally on each side, the middle portion is formed by the massed heads of the sperms and posteriorly are the long tails (Figs 78, 79, T) which propel the bundle along by rhythmic beating

Each sperm tube has a short vas efferens (Fig. 82, VE). These ducts form the centre of the testis and unite posteriorly to form the vas deferens (Fig. 80, VD), the anterior part of which consists of a single greatly coiled duct, the epididymus. This duct leaves the testis from its posterior and passes posteriorly to the vesiculae seminales (Fig. 80, VS). The vesiculae, which are paired and have a lobed appearance, consist of both large and small tubules or accessory glands, used for storage of mature sperm The larger tubules form the major portion of the vesiculae and the smaller ones, in the posterior portion, are partly covered by the larger ones. The vesiculae open by several tubules into the dorsal side of the large, median, unpaired, thick walled ductus ejaculatorius (Figs 80, 81, DE), the ventral surface of which opens into the bifid penis (Fig. 80, PN). Each lobe of the penis has a constriction near the more distal portion of the organ

Nervous System

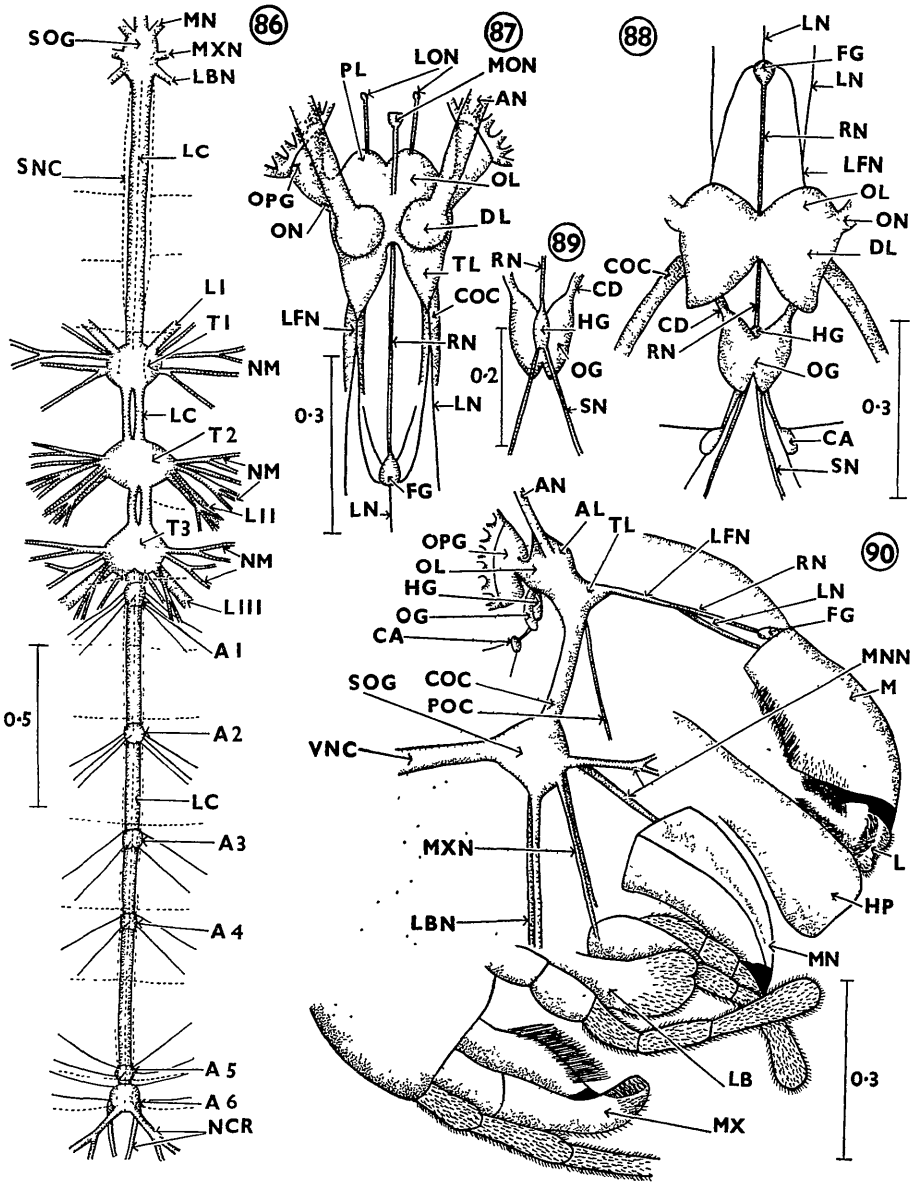
The nervous system of *Macropathus filifer* can be divided into the central nervous system and the sympathetic nervous system.

Central Nervous System

This consists of the brain and a double series of ganglia joined by longitudinal connectives.

Brain. The brain lies dorsal to the oesophagus between the supporting arms of the tentorium and consists of three parts—the protocerebrum, deutocerebrum and tritocerebrum respectively The protocerebrum innervates the compound eyes and ocelli and is divisible into two, the protocerebral lobes (Fig. 87, PL) and the optic lobes (Fig. 88, OL). The protocerebral lobes send off three ocellar nerves each terminating in an ocellar ganglion Only the median ocellus remains as functional in *M. filifer* with a well developed nerve (Fig. 87, MON) and ganglion. The two lateral ocelli have disappeared externally, however, proof that they did once exist is given by the vestigial pair of lateral ocellar nerves (Fig. 87, LON) with their poorly developed ganglia The optic lobes give rise to the two optic nerves (Fig. 87, ON) These swell into the moderately developed optic ganglia (Fig. 87, OPG) which are connected to the compound eyes by a layer of post-retinal fibres The deutocerebrum is composed of the large paired antennary, or olfactory lobes (Figs 87, 88, DL), which give rise to the stout antennary nerves (Fig 87, AN) innervating the long antennae. The tritocerebrum is well developed in *Macropathus* in contrast to its poor development in both *Hemideina* and *Periplaneta* It consists of two widely separated pear-shaped lobes (Fig. 87, TL) joined together by the post-oesophageal commissure (Fig. 90, POC) which passes immediately behind the oesophagus. From the tritocerebrum arise the paired circumoesophageal connectives (Figs 87, 88, 90, COC) which pass ventrally, on either side of the oesophagus, to the suboesophageal ganglion (Fig. 90, SOG) Each lobe also gives rise to the labrofrontal nerve (Figs 87, 88, LFN) which divides into two, a short distance from its origin, the outer nerve passing to the labrum (Fig. 87, LN) and the inner one curving inwards to join the frontal ganglion (Fig. 87. FG), which also sends a branch to the labrum (Figs. 87, 88, LN).

The suboesophageal ganglion, which is connected to the brain by the circumoesophageal connectives, gives off paired nerves to supply the labium (Fig. 90, LBN), maxillae (Fig 90, MXN) and mandibles (Fig 90, MN), and



TEXT-FIG. 18—*Nervous System* (Scale in cm) FIG 86—Central nervous system FIG 87—Frontal view of brain FIG 88—Posterior view of brain showing sympathetic system FIG 89—Ventral view oesophageal ganglia showing hypocerebral ganglion. FIG 90—Head opened up to show lateral view of brain and suboesophageal ganglion with nerves to mouth parts

A1, A2, A3 A4, A5, abdominal ganglia, AN, antennary nerve, CA, corpus allatum CD connective to deutocerebrum, COC, circumoesophageal connective, DL, deutocerebral lobe, FG, frontal ganglion, HG, hypocerebral ganglion, HP, hypopharynx, L, labrum; LI, LII, LIII, leg 1, 2, 3, LB, labium, LBN, labial nerve LC, longitudinal connective LFN labro-frontal nerve LN, labial nerve, LON, lateral ocellar nerve, MN, mandible, MNN mandibular nerve, MON, median ocellar nerve, MX, maxilla, MXN, maxillary nerve, NCR, nerve to cercus and reproductive organs, NM, nerves to muscles, OG oesophageal ganglion, OL, optic lobe, OPG, optic ganglion, PL, protocerebral lobe; POC, post-oesophageal commissure; RN, recurrent nerve SN stomatogastric nerve SNC, sympathetic nerve cord, SOG, suboesophageal ganglion, T 1, T 2, T 3, thoracic ganglia 1, 2, 3, TL, tritocerebral lobe, VNC, ventral nerve cord

also a pair of long connectives (Fig. 90, VNC) which pass back under the tentorium, through the occipital foramen and neck to the first thoracic ganglion.

Ventral Nerve Cord Fig 86. It consists of three thoracic and six abdominal ganglia connected by paired longitudinal connectives (LC) into a long chain extending the whole length of the body. From each thoracic ganglion arise several pairs of nerves, which supply the muscles of the corresponding segment. Each ganglion gives rise to a large pair of nerves, which innervate the legs (LI, LII, LIII). In the abdominal ganglia, a gradual reduction in number from six to four can be seen taking place. The first abdominal ganglion (A1) has moved forward into the thorax and lies just anterior to the metafurca, so that it has nearly fused with the third thoracic ganglion (T3). The second (A2), third (A3), and fourth (A4) abdominal ganglia are equidistant from each other, but the fifth ganglion (A5) has moved posteriorly so that it is nearing fusion with the sixth abdominal ganglion (A6). In the various specimens of *M. filifer* examined it was noted that the third thoracic and first abdominal ganglia, and the fifth and sixth abdominal ganglia were closer together in some wetas than in others, showing that the process of reduction is actively taking place. The second, third, fourth and fifth abdominal ganglia are approximately the same size, but the first ganglion is slightly larger than these others. From the first and second abdominal ganglia arise three pairs of nerves, and from the third, fourth and fifth ganglia two pairs of nerves are given off. These nerves pass to the abdominal muscles in each segment. This differs from *Hemideina* where there are two pairs of nerves from the first abdominal ganglion and one pair from the second, third, fourth and fifth abdominal ganglia; and from *Periplaneta* where there are two nerves from each abdominal ganglion. The sixth ganglion, which is the largest, is composite in structure, being composed of the fused ganglia of the posterior segments. It gives off several nerves to the muscles and cerci; and to the ovipositor, ovaries and spermatheca in the female, and the vesiculae seminales in the male (NCR).

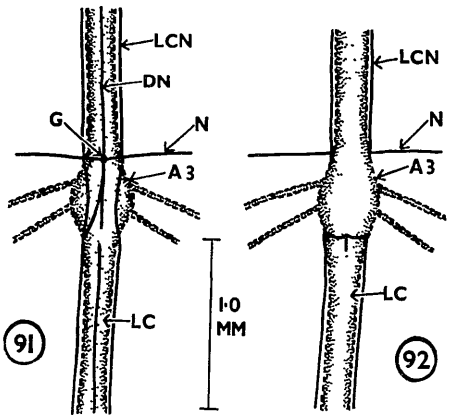
Sympathetic Nervous System

This is well developed in *Macropathus filifer* and is divided into the oesophageal sympathetic (stomatogastric) and the ventral sympathetic systems.

Oesophageal Sympathetic System. From the tritocerebrum two frontal nerves pass forwards to the frontal ganglion (Fig. 87, FG). Anteriorly the ganglion gives off a nerve to the labrum (Fig 87, LN) and posteriorly it gives off a recurrent nerve (Figs. 87, 88, 89, RN) which passes back, dorsal to the oesophagus and ventral to the brain, to the hypocerebral ganglion (Figs. 88, 89, HG). From the hypocerebral ganglion two stomatogastric nerves (Figs. 88, 89, SN) pass backward on either side of the crop to the junction of the crop and gizzard, where each terminates in a stomachic ganglion from which numerous nerves pass to the crop and gizzard. In *Hemideina,* according to Maskell (1927), the hypocerebral ganglion is hidden from view by a pair of oesophageal ganglia which lie over it These can be separated, when the hypocerebral ganglion is exposed and is seen to be connected with each oesophageal ganglion. In *Macropathus* this process has progressed one step further. The hypocerebral ganglion is hidden by the oesophageal ganglia (Fig. 88, OG) as in *Hemideina*, but here the oesophageal ganglia have fused medianly, so that the hypocerebral ganglion cannot be exposed to view Because of this fusion,

the hypocerebral ganglion is connected antero-medianly to the oesophageal ganglia (Fig. 89), and not separately to each ganglion The oesophageal ganglia are each connected anteriorly to the deutocerebrum Posteriorly a fine nerve arises from each and passes back to two small, oval bodies, the corpora allata (Fig. 88, CA), which, according to Imms (1946), were formerly referred to as posterior oesophageal ganglia. They are now regarded as ductless glands, which secrete hormones concerned in regulating growth.

Ventral Sympathetic System. In *M filifer* from the suboesophageal ganglion (Fig. 86, SOG) to the sixth abdominal ganglion (Fig 86, A6), three fine longitudinal nerves lie one dorsal to and one on either side of the ventral nerve cord. The three nerves pass posteriorly from the suboesophageal ganglion, the two lateral ones each giving off two branches, while the dorsal nerve gives off a pair of lateral nerves just anterior to the first thoracic ganglion (Fig. 86, T1), and terminates on the antero-dorsal portion of that ganglion On each of the first thoracic and first to fifth abdominal ganglia the two lateral nerves loop over the sides of each ganglion to unite below the antero-ventral surface of each respective ganglion From the second thoracic (Fig 86, T2) ganglion arise a



TEXT-FIG 19 *Sympathetic Nervous System* FIG 91—Enlarged dorsal view of sympathetic system on third abdominal ganglion and part of ventral nerve cord FIG 92—Enlarged ventral view of sympathetic system in same region

A3, third abdominal ganglion, DN, dorsal sympathetic nerve, G, sympathetic ganglion, LC longitudinal connective, LCN, lateral sympathetic nerve, N, sympathetic nerve to spiracle

pair of nerves going to the metathoracic spiracles The nerves from the third thoracic ganglion (Fig. 86, T3) swell into a pair of ganglia, each of which gives off two nerves, one to the first abdominal spiracle and one to the first abdominal ganglion (Fig 86, A1) In the first five abdominal ganglia the sympathetic system follows the same pattern, the two lateral nerves (Figs 91, 92, LCN) loop over each side of their respective ganglion, while the dorsal nerve (Fig. 91, DN) passes three-quarters of the way down the ganglion and then turns to the left and fuses with the left lateral nerve The two lateral nerves unite on the antero-ventral surface of the ganglion (Fig 92) and give off three nerves which pass back to the next ganglion The dorsal nerve runs back along the ventral surface of the ganglion and then passes dorsally to the upper surface of the longitudinal connectives near their anterior point of origin In the sixth abdominal ganglion the dorsal nerve does not fuse with the left lateral nerve but ends on the anterior part of the ganglion The two lateral

nerves loop over the sides of the ganglion, unite antero-ventrally, and give off a median branch, which passes postero-ventrally under the ganglion and then curves back antero-dorsally to the middle of the ganglion From the abdominal sympathetic nerve cord arise seven pairs of nerves which pass to the abdominal spiracles. This system appears to be much more strongly developed in *Macropathus* than in *Hemideina,* where there is only a dorsal nerve passing from the suboesophageal ganglion to the sixth abdominal ganglion and no lateral nerves.

General Discussion

Macropathus filifer is a member of the Orthoptera, an order with a long fossil history, and therefore it is not surprising that it should possess a number of primitive characters. Very little work has been done on the anatomy and morphology of the members of the group, so that it is hard to relate the various structures found in *M. filifer.* Perhaps the most extensive worker in this field has been R. E. Snodgrass, who has worked more particularly on the Acridiidae. L. Chopard and E. M. Walker have both made comparative studies of the external genitalia of Orthoptera, and N. Ford has done similar work on their muscles.

The possession of a hypognathous head with the longitudinal axis being vertical, while the mouth parts are directed ventrally, is considered by Snodgrass (1935a) to be a more primitive condition than the prognathous head, where the longitudinal axis is horizontal and the mouth parts are directed anteriorly. This is in direct opposition to Walker (1932) who considers prognathism to be the more primitive of the two; but it appears to me, after finding several other primitive features in *M. filifer,* that Snodgrass is correct and the possession of a primitive condition in the head would be a perfectly logical conclusion.

The circulatory system is of the same primitive pattern found in other members of the Orthoptera. In most insects the heart is restricted to the abdomen where it is variously shortened, so that there are usually fewer chambers than abdominal segments, sometimes only one. In *M filifer,* however, the heart extends into the prothorax from where it is continued as the aorta into the head. It consists of eleven chambers marked off from each other by constrictions and each possessing a pair of laterally placed ostia Although *Periplaneta* possesses thirteen chambers, which is the most primitive condition recorded for insects, the possession of eleven in *Macropathus* shows that very little reduction in the number of chambers has taken place. Corresponding with the number of chambers present are the eleven pairs of alary muscles As the number of pairs of these muscles found in insects ranges from twelve in *Periplaneta* to two in the larva of *Chironomus,* the possession of ten pairs by *Macropathus* is definitely a primitive condition.

The respiratory system of *M. filifer* belongs to the Holopneustic system, where all ten spiracles are open. This, according to Imms (1946), is recognised as the most primitive type in insects. The system consists of six longitudinal trunks—two dorsal, two lateral, and two ventral, the dorsal and ventral trunks being connected to the lateral ones by transverse connectives

The typical insect head is composed of a number of sclerites, joined together by sutures. In *M. filifer* several of these sclerites have become fused together and the epicranial, frontogenal and epistomal sutures have disappeared. Dorsolaterally the gena is separated from the vertex by a suture running from the

compound eye to the occipital suture, the geno-epicranial suture, which is unlike anything found in other Orthopterans so far described. It is possible to speculate that these two sutures on either side of the head are another very primitive condition of *M. filifer* representing the beginnings of the epicranial suture. As the Insecta evolved, these sutures moved dorsally till they met and fused in the mid-dorsal line as the epicranial suture, so common in most members of the Orthoptera and other groups of insects. The presence of this suture cannot be related back to the Myriapods because there the head capsule is a fused box lacking sutures. If the embryology of *M filifer* was worked out it would probably reveal the answer to this problem. However, the fact that several of the common sutures of the insect head are not present here suggests that the head capsule is not primitive and that these peculiar sutures have been secondarily acquired.

The lack of wings in *M filifer* has had a marked effect on the structure of the thorax. The pleural wing process is lacking from each segment and consequently the muscles associated with the wings are missing also, so that the greater part of the thorax is filled with muscles for operating the legs The apodemes for muscle attachment in the sternum differ in several ways from other members of the Orthoptera The postfurcasternite present in most insects is absent in *M. filifer* and the prosternite, although present in the prosternum, is absent from the meso- and metasterna. Perhaps the most important difference is the presence of a small spinasternite with a well developed spina in the metasternum, where it forms the last sclerite of the segment. Snodgrass (1935a) has stated, "It should be observed that the metasternum never has a spinasternite, because the third intersternite either is suppressed or becomes the acrosternite of the first abdominal sternum". As practically no work has been done on morphology in the Gryllacridoidea it is possible that a spinasternite is present in other members of the group, although this is the first time it has been recorded.

Whether lack of wings in *M filifer* is a primitive condition or secondarily acquired is open to discussion According to Imms (1937), "The earliest fossil remains of insects found in Carboniferous rocks were exopterygote forms endowed with large and tolerably efficient wings Along with them are fragments of contemporaneous nymphs, thus indicating that these insects underwent incomplete metamorphosis". In another part he says, "We are still faced with want of direct evidence from fossils with regard to the two most important problems of insect phylogeny—viz, the origin of the insects as a class, and the origin of wings". The Protorthoptera which were the ancestors of the cursorial and saltatorial Orthoptera occurred in the upper Carboniferous and show from the structure of their thorax that they had developed "some capacity for running". One member of this group, *Oedischia* Brongn., exhibits the characters of a primordial long-horned grasshopper From this it would appear that in the Orthoptera the earliest members of the group were winged and these ancestral forms gave rise to both winged and wingless forms The earliest fossil remains of the Rhaphidophoridae so far recorded are from the Oligocene in Europe, *Prorhaphidophora* Chopard, 1936, from the Amber of the Baltic, showing it to be similar in structure to members of the family existing to-day Thus loss of wings must have taken place at some earlier stage in their geological history. Examination of *M filifer* has shown that there is no trace of any vestigial structure which could be connected with the possession of wings in

the past, but it is possible a study of the embryology may throw some light on the subject.

The alimentary system of *M. filifer* conforms in its general plan with that of the two other members of the Gryllacridoidea that have been studied—namely *Hemideina* and *Stenopelmatus*. However, there are several small points in which it is peculiarly distinctive. The presence of four hundred and fourteen teeth in the gizzard, one hundred and sixty-two primary and two hundred and fifty-two barbated lobes, as compared with two hundred and sixteen in *Stenopelmatus fuscus*, one hundred and thirty-eight primary and fifty-two barbated lobes, and one hundred and twenty primary teeth in *Hemideina thoracica*, is of interest because of the much greater number in *Macropathus filifer;* but comparison of the shape of the primary teeth reveals a difference in structure and shape In both *Hemideina* and *Stenopelmatus* the primary teeth are triangular in shape and flattened apically, while in *Macropathus*, although the superficial appearance is triangular, the teeth are really ovoidal with three pairs of elongate lateral projections. These projections are covered with a thick layer of chitin and contain connective tissue and longitudinal muscle. Unlike the teeth of *Hemideina* and *Stenopelmatus*, which are solid, they possess a large central cavity. As far as is known the peculiar structure of the primary tooth is characteristic of *Macropathus*

Another peculiarity is the presence of a "gland organ" in the rectum similar to that recorded for the first time in insects by Davis (1927) as occurring in *Stenopelmatus* Although differing in minor details in their structure, the basic pattern in the two insects is the same and they probably have a similar function *Stenopelmatus* and *Macropathus* do not share the same type of habitat, *Stenopelmatus* frequenting semi-arid areas, while humidity is essential to *Macropathus*. Davis has suggested that the organ may either function as a mucus-gland or be used to remove excess water from the faeces. The latter function would only be of use where conservation of water is necessary, and as *Stenopelmatus* is found in semi-arid localities it was a natural conclusion for Davis to come to. However, as *Macropathus* lives under humid conditions, and yet has a similar organ, the need for conservation of water would not be so vital. Thus it seems far more probable that the "gland" functions by secreting mucus to assist in the expelling of faeces Further comparative studies of the alimentary tracts of other members of the Orthoptera may help to solve this problem

The reproductive system of *M. filifer* conforms in most respects with that described for other members of the *Orthoptera* The two main differences are found in the female system Here there is a little flap of tissue attached to the base of the sub-genital plate which, during copulation, may be used to close the vaginal aperture so that spermatozoa, being unable to pass up that way, must go to the spermatheca for storage The other difference is that the spermatheca, unlike that found in most insects, does not open into the vagina, but opens instead on to the lower surface of the copulatory chamber Thus it is not till the egg is on its way to the exterior that it becomes fertilized. There seems to be no real reason for this peculiarity in *Macropathus*, as it is neither an advantage nor a disadvantage to the insect

The nervous system of *Macropathus* is of interest because it has become more complex in structure As the insect avoids bright light, vision is not so essential

to it. Thus the ocelli have degenerated, and although the median one is still well developed, both internally and on the surface of the head capsule, the two lateral ocelli have become vestigial. They have completely disappeared from the head capsule, but two small nerves terminating in poorly developed ganglia can be observed arising from each of the protocerebral lobes of the brain With gradual loss of sight, the sense of touch has become correspondingly well developed and therefore the antennary nerves are very robust.

The abdominal ganglia in insects are variable in number, ranging from eight in *Machilus* and the larvae of many insects, to complete fusion of all the ganglia into one large composite ganglion situated in the thorax as in *Musca*. In most Orthoptera there are six abdominal ganglia, the sixth ganglion being composed of the fused ganglia of the posterior segments It is interesting to observe that in *M. filifer* there is a tendency towards a gradual reduction in the number of ganglia present. The first abdominal ganglion has moved forward into the thorax so that it has nearly fused with the third thoracic ganglion, while the fifth and sixth abdominal ganglia have become correspondingly close together. In the various specimens of *M. filifer* examined, it was noticed that these two pairs of ganglia were closer together in some insects than in others

Another development is in the oesophageal sympathetic system, where the oesophageal ganglia have become fused medianly and the hypocerebral ganglion is connected antero-medianly with them. This is an advance on *Hemideina* where, although the hypocerebral ganglion is hidden from view by the oesophageal ganglia, they can be separated and the hypocerebral ganglion is then seen to be joined separately to each. Imms (1946) says, "In the Blattidae and certain other families the hypocerebral ganglion is more or less atrophied", and it appears that this is in the process of taking place in *M filifer*.

From this it can be seen that although *M. filifer* could be classed as a primitive insect, it has also become secondarily modified in a number of different ways, partly along the general lines of insect evolution, and partly by becoming adapted to its environment.

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